

UNIVERSIDAD COMPLUTENSE DE MADRID

FACULTAD DE CIENCIAS GEOLÓGICAS

Departamento de Paleontología



TESIS DOCTORAL

**Paleobiogeografía, cambios climáticos globales y macroevolución en
aves no passeriformes: patrones de radiación, dispersión y adaptación
durante el Cenozoico**

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

Jonathan S. Pelegrin Ramírez

Directores

Manuel Hernández Fernández

Juan López Cantalapiedra

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PALEOBIOGEOGRAFÍA, CAMBIOS CLIMÁTICOS GLOBALES Y MACROEVOLUCIÓN EN AVES NO PASERIFORMES: Patrones de radiación, dispersión y adaptación durante el Cenozoico

*Paleobiogeography, global climate changes and macroevolution in non-passerine birds:
Radiation, dispersal and adaption patterns during the Cenozoic.*



JONATHAN S. PELEGRIN RAMÍREZ

TESIS DOCTORAL

Ph.D. Thesis

Directores:

Dr. Manuel Hernández Fernández

Dr. Juan López Cantalapiedra



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Tesis Doctoral presentada por
JONATHAN S. PELEGRIN RAMÍREZ

Directores de Tesis
Dr. MANUEL HERNÁNDEZ FERNÁNDEZ
Dr. JUAN LÓPEZ CANTALAPIEDRA



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Memoria de Tesis Doctoral presentada por
JONATHAN S. PELEGRIN RAMÍREZ

Bajo la supervisión de los doctores:
MANUEL HERNÁNDEZ FERNÁNDEZ Y JUAN LÓPEZ CANTALAPIEDRA



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Instituto de Geociencias – IGEO



Departamento de Geología Sedimentaria y Cambio Medio Ambiental

VºBº Director de Tesis
Manuel Hernández Fernández

VºBº Director de Tesis
Juan López Cantalapiebra

Fdo.
Jonathan S. Pelegrin Ramírez



Charles Darwin (1836)

A Tita...

Species evolve exactly as if they were adapting as best they could to a changing world, and not at all as if they were moving toward a set goal.

George Gaylord Simpson (1902-1984)

Science is more than a body of knowledge. It's a way of thinking, a way of skeptically interrogating the universe.

Carl Sagan (1934-1996)

The Homo sapiens also ranks as a "thing so small" in a vast universe, a wildly improbable evolutionary event, and not the nub of universal purpose. Make of such a conclusion what you will. Some people find the prospect depressing. I have regarded such a view of life as exhilarating-a source of both freedom and consequent moral responsibility. We are the offspring of history, and must establish our own paths in this diverse and interesting of conceivable universes-one indifferent to our suffering and therefore offering us maximal freedom to thrive or to fail, in our own chosen

Stephen Jay Gould *Rock of Ages* (1999)

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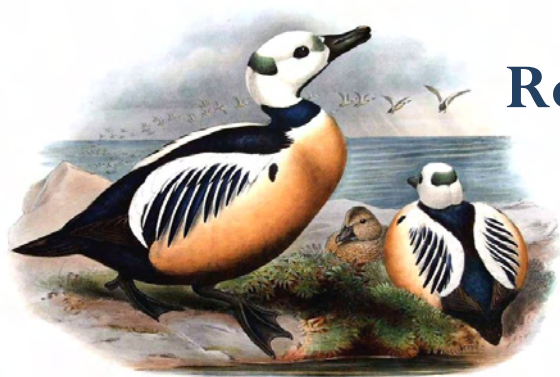


Breve prefacio

Con cerca a 10.000 especies en la actualidad, las aves representan uno de los grandes hitos en la evolución de los vertebrados. Su historia comenzó hace 150 Millones de años. Sin embargo, fue realmente a finales del Cretácico cuando llegó la oportunidad histórica que permitiría a las aves modernas evolucionar hasta el grupo que son hoy día y demostrarnos así que los dinosaurios siguen tan vivos como antaño. El destacado éxito evolutivo que alcanzaron se debe fundamentalmente a muchas adaptaciones desarrolladas a partir de una amplia diversidad de morfologías, dietas y una prominente capacidad voladora. El destacado desarrollo de estas características habría desempeñado un importante papel en el proceso de colonización de diferentes continentes y sus biomas en diversos periodos a lo largo del Cenozoico, alcanzando en la actualidad una amplia presencia en todos los ecosistemas de la tierra: desde las selvas lluviosas en los trópicos hasta las tundras árticas, lugares en donde son un componente esencial de las comunidades y sus entramados tróficos. Teniendo en cuenta la importancia del estudio de la avifauna como un elemento clave de la biodiversidad, esta Tesis Doctoral, integrando un marco neontológico y paleontológico, pretende reconstruir, empleando diversas metodologías, este recorrido por la historia evolutiva de las aves para conocer cómo los diferentes procesos de cambios físicos globales han influido en su evolución, configurando de esta manera la diversidad que vemos en nuestros días.

Resumen - Abstract





Resumen

PALEOBIOGEOGRAFÍA, CAMBIOS CLIMÁTICOS GLOBALES Y MACROEVOLUCIÓN EN AVES NO PASERIFORMES: PATRONES DE RADIACIÓN, DISPERSIÓN Y ADAPTACIÓN DURANTE EL CENOZOICO

Introducción

Desde su origen en el Jurásico, las aves adquieren una preponderancia en los ecosistemas alcanzando cerca de 10000 especies en la actualidad, una diversidad sin parangón entre los vertebrados terrestres. Desde los comienzos de las ciencias naturales, las aves fueron uno de los grupos animales más estudiados, lo que las ha llevado a ser sin duda uno de los mejor conocidos en términos de su ecología y distribución geográfica. En los últimos años, esta vasta acumulación de conocimiento ha posibilitado el surgimiento de nuevos análisis para conocer sus patrones de diversidad y las causas subyacentes a los mismos. Sin embargo, a pesar de la abundancia de trabajos relacionados con diversos aspectos de su biología y el creciente auge de la aplicación de técnicas moleculares, son pocos los trabajos que integren las diversas fuentes de información en una perspectiva macroevolutiva. Asimismo, muchos trabajos suelen considerar el registro fósil de las aves como deficiente o poco representativo, siendo también escasos los estudios paleoecológicos con implicaciones sobre la evolución de este grupo.

Considerando lo anterior, esta tesis doctoral se plantea como objetivo fundamental determinar cómo los diversos patrones y procesos macroevolutivos de las aves modernas (Neornithes) han sido influidos por los cambios climáticos y procesos geológicos que han acaecido en la Tierra a lo largo del Cenozoico. Por lo tanto, el presente proyecto de tesis se constituye como un reto importante en la integración de toda la información disponible para construir un marco histórico que logre explicar procesos evolutivos de innovación adaptativa responsables de la importante disparidad ecológica que observamos actualmente en las aves. La disparidad morfológica que presentan los diversos clados ha sido producto de la adaptación a diversos regímenes

dietarios y por ende esta tiene un vínculo directo con los procesos macroecológicos y macroevolutivos del ambiente donde se desarrollaron.

Los análisis de los diversos procesos ecológicos y evolutivos que han configurado la diversidad que observamos en las aves fueron abordados desde una visión filogenética y abarcando una escala taxonómica desde el nivel de especie, hasta el de familias y órdenes. Las diversas escalas de estudio nos permitieron utilizar aproximaciones nuevas e inferencias macroevolutivas en un contexto espacio-temporal amplio y a la vez detallado. Lo anterior fue posible gracias a la conjunción de metodologías clásicas que serían probadas por primera vez para aves, así como la aplicación de nuevos métodos de análisis que integran las relaciones filogenéticas, la historia paleoclimática y paleoecológica, y el registro fósil en un marco paleobiogeográfico.

Síntesis

La hipótesis del uso de los recursos propuesta por E.S. Vrba establece un escenario macroevolutivo que conecta ecología (grado de especialización en la ocupación de biomas), cambios físicos ambientales a gran escala y eventos de especiación y extinción. Esta hipótesis, originalmente constituida a partir de estudios con faunas de mamíferos del Neógeno-Cuaternario africano, propuso un sólido marco explicativo de sus procesos evolutivos. En el capítulo 2 de esta tesis doctoral se evalúa por primera vez la validez de esta hipótesis a partir de los datos derivados de todas las especies actuales de aves no paseriformes ($N = 3951$). Para esto, nuestros análisis se basaron en comparar los patrones de distribución observados para las ocupación de los biomas por parte de distintas especies con un escenario donde la ocupación de los biomas sigue un patrón aleatorio y por lo tanto, la especialización ecológica en biomas no influye en dicha distribución (modelo nulo).

Los resultados alcanzados son consistentes con lo propuesto por la hipótesis del uso de los recursos, la cual fue analizada sobre sus tres premisas fundamentales. La primera propone que a causa de sus mayores tasas de especiación y extinción, existirá una mayor proporción de especies especialistas de bioma que de generalistas. Por su parte, la segunda premisa establece que debido a sus características ecológicas, ciertos clados tenderán a ser más especialistas con respecto a otros. Este aspecto fue ampliamente respaldado por nuestros hallazgos, en estos, los clados faunívoros presentaron una tendencia a ser más generalistas que los herbívoros, con los omnívoros

en una posición intermedia. De igual modo, la migración mostró ser una importante estrategia adaptativa que favoreció la ocupación y diversificación de diversos linajes en ambientes hostiles y en contra de los supuestos iniciales no afectó las tendencias generales. Finalmente, la tercera premisa establece que existirá una prevalencia de especies especialistas en la pluvisilva, el desierto, la estepa y la tundra, biomas que representan extremos del gradiente climático terrestre y son altamente susceptibles a los procesos de reducción-fragmentación y expansión durante los periodos de cambio climático. Por tanto, dichos biomas constituyen importantes escenarios de especiación y extinción. Aunque no se contemplaban dentro de las premisas de la hipótesis, también se obtuvieron importantes evidencias de la influencia de los gradientes altitudinales en los trópicos, la heterogeneidad de hábitat y los eventos faunísticos del Neógeno en los patrones macroevolutivos de las aves.

En el capítulo 3 se realizó un análisis que consideró las relaciones filogenéticas de todas las aves actuales y sus parientes fósiles mejor conocidos. Este sería el punto de partida que permitió establecer diversos escenarios paleobiogeográficos (modelos) teniendo en cuenta los cambios tectónicos y climáticos que ha sufrido la Tierra a lo largo de la evolución de las aves actuales. Debido a que sin duda el vuelo y sus diversas variaciones han sido claves en el éxito evolutivo que de las aves, los diversos escenarios paleobiogeográficos fueron analizados de acuerdo con diferentes capacidades de dispersión que tienen en cuenta la historia particular de cada uno de los grandes clados de Neornithes. De acuerdo con lo anterior, se estableció estadísticamente el escenario biogeográfico más probable para cada clado y para todas las aves no passeriformes a través de una nueva metodología que permitió integrar gran cantidad de información paleogeográfica, paleoclimática, fósil y reciente.

De acuerdo con los resultados obtenidos, la evolución inicial de las primeras Neornithes estaría asociada a Sudamérica. Los modelos con mayor probabilidad sugieren que este continente habría jugado un papel clave como refugio durante los periodos de importante cambio ambiental que sucedieron durante el Cretácico Superior y que ocasionaron la extinción de otros linajes de vertebrados. De esta manera, a lo largo de la historia evolutiva de las Neornithes, diversos eventos de dispersión y colonización habrían sido fundamentales para posteriores procesos de vicarianza y diversificación dentro de diferentes linajes. El primer evento destacado habría sucedido durante el Cretácico superior donde los ancestros de importantes

linajes cursoriales y acuáticos como Paleognathae, Galloanseres y Aequornithes se dispersan desde Sudamérica hacia África, la Antártida y Norteamérica. Asimismo, según nuestros resultados, una segunda ola de diversificación se habría producido a finales del Paleoceno y comienzos del Eoceno. Este evento habría sido protagonizado principalmente por linajes de aves arborícolas y con destacada capacidad voladora, como diversas familias dentro de Caprimulgiformes y Afroaves. Los patrones observados sugieren una posible relación entre estos procesos y la expansión de los ecosistemas tropicales hacia altas latitudes durante este periodo. Posteriormente, durante el Oligoceno importantes cambios globales, con la aparición de nuevas configuraciones oceanográficas y biomas abiertos debido a las tendencias de enfriamiento global, serían factores condicionantes en la transformación de muchos ecosistemas. Según lo anterior, nuestros resultados sugieren que la creación de nuevos nichos generó un destacado pulso de dispersión en linajes marinos y terrestres. Durante este periodo, muchas aves playeras y marinas (Charadriiformes y Procellariiformes), así como los linajes modernos de Galliformes, Otidiformes, entre otros adaptados a ambientes abiertos, presentarían una prominente diversificación. Finalmente, durante el Mioceno superior y el Plioceno, con la intensificación del régimen estacional en el Hemisferio Norte, importantes eventos de contracción y retracción de los bosques tropicales hacia latitudes ecuatoriales causarían la extinción de diversas familias en los emergentes ambientes templados estacionales y las confinarían a sus distribuciones pantropicales actuales.

En el capítulo 4 se explora cómo se han configurado los patrones de ocupación de los diversos biomas desde una perspectiva filogenética. Esto permitió integrar la conservación del nicho al contexto explicativo de la dinámica biómica. Como quedaría patente en el capítulo 2, los biomas se consolidan como unidades ecológicas claves para estudios macroevolutivos y macroecológicos, debido a que su estructura e historia están estrechamente ligadas a cambios climáticos y geológicos. Igualmente, la señal filogenética implícita en la evolución de los taxones ofrece la posibilidad de estudiar a través de nuevas técnicas de análisis los patrones históricos de la ocupación y diversificación de las aves en estas “arenas evolutivas”.

Galliformes y Falconiformes son dos grupos con una marcada y amplia presencia en los ecosistemas terrestres. Del mismo modo, estos grupos han desarrollado unas adaptaciones ligadas a dos estrategias tróficas diferentes como herbívoros y faunívoros

respectivamente. El amplio conocimiento de sus relaciones filogenéticas a nivel de especie y su información ecológica permitió abordar el estudio de su dinámica histórica en la ocupación de biomas. Esto posibilitó la obtención de modelos macroevolutivos para conocer qué factores y cambios ambientales fueron fundamentales en la ocupación de los diferentes biomas, y si existen tendencias comunes en los grupos a pesar de sus diferencias ecológicas. Estas aproximaciones también hicieron posible arrojar mayor luz sobre cuáles son las principales tendencias en la evolución del nicho climático respecto a la ocupación de ciertos ambientes mediante la evaluación del concepto de conservacionismo filogenético de bioma.

Los resultados del capítulo 4 muestran una amplia consistencia con el principio de la conservación de nicho para ambos grupos, siendo estadísticamente preponderante en la mayoría de los biomas, y especialmente marcado en los biomas extremos dentro del gradiente climático. Estos hallazgos reflejan el importante desarrollo de unos ajustes fisiológicos y morfológicos para la invasión de ciertos biomas, muchas de estas a su vez tendieron a posibilitar posteriores colonizaciones, como es el caso de las adaptaciones a climas fríos. Igualmente, los diversos cambios climáticos acaecidos durante el Mioceno habrían sido fundamentales en los patrones de diversificación de ambos grupos. Durante este periodo, la adaptación y amplia ocupación de biomas secos y estacionales como el bosque seco tropical y la sabana, habría permitido la posterior colonización de otros biomas, tanto tropicales como templados. Finalmente, para ambos grupos el bosque seco tropical resulta desempeñar un rol clave para sus procesos de diversificación.

Conclusiones

En general, nuestros resultados ofrecen una visión holística del importante papel que han desempeñado los cambios climáticos globales y los procesos tectónicos en la configuración de la diversidad y disparidad moderna de las aves no passeriformes. Nuestra aproximación evidencia cómo a través del estudio de las faunas actuales y sus relaciones filogenéticas pueden obtenerse inferencias macroevolutivas de gran poder explicativo. Finalmente, este estudio abre una nueva perspectiva que integra información neontológica y paleontológica en un contexto histórico para entender y arrojar mayor luz a la compleja evolución de las aves modernas desde su origen a nuestros días.



Abstract

PALEOBIOGEOGRAPHY, GLOBAL CLIMATE CHANGES AND MACROEVOLUTION IN NON-PASSERINE BIRDS: RADIATION, DISPERSAL AND ADAPTION PATTERNS DURING THE CENOZOIC

Introduction

Since their origin in the Jurassic period, birds have acquire an important role in Earth ecosystems with an outstanding diversity of near 10,000 species among modern terrestrial vertebrates. During the early history of natural sciences, birds were one of the most studied biological groups. As a result, birds are one of the best-known animal groups in terms of their ecology and geographic distribution. This vast accumulation of knowledge has enabled the emergence of new analyses to understand their diversity patterns and their underlying triggering factors. However, despite the relative abundance of studies about diverse aspects of their biology and the growing availability of molecular phylogenetic trees, we still lack comprehensive perspectives on some key aspects of their macroevolution. Also, many studies usually consider the bird fossil record as deficient or under-representative; due to this, there are few studies about paleoecology and evolutionary implications in this group.

In this context, this thesis has the aim of determining the influence of past climate changes and geologic processes in the macroevolutionary patterns of modern birds lineages (Neornithes) along the Cenozoic. In addition, this thesis project represents itself a challenge in the integration of all available information to generate a historical framework and explain evolutionary key innovations that allowed the ecological disparity that we observe in living birds. The broad morphological disparities among bird clades are the product of adaptation to different dietary regimes.

Undoubtedly, this morphological diversity has a link with ecological and evolutionary processes in the environments where bird lineages developed.

The study of the evolutionary processes that rendered the diversity of living birds was addressed under a phylogenetic perspective considering a broad taxonomic scale: from species level to families and orders. The diverse study scales allow us to employ new approaches and macroevolutionary inferences in a broadly spatial and temporal scope, but also with a significant detail level. In short, we integrated classic and new methodologies, which were tested for first time in birds in a macroevolutionary context, and combined phylogenetic information, paleoclimatic and paleoecological history, as well as vast information from the fossil record in an integrative paleobiogeographical frame.

Synthesis

The resource-use hypothesis proposed by E.S. Vrba establishes a connection between ecology (specialization in the occupation of biomes), large-scale physical changes of the environment (climate, tectonics, etc.) and speciation and extinction events. This hypothesis, originally formulated for African Neogene-Quaternary mammalian faunas, proposed a robust framework to explain the evolutionary processes. In Chapter 2 of this dissertation, the validity of this hypothesis is evaluated here for all the species of non-passerine birds ($N = 3951$) for the first time. In particular, we compared the observed distribution patterns of the different species in the current biomes respect to a null scenario generated randomly.

The results obtained are consistent with the three fundamental premises of the resource-use hypothesis. The first one suggests that due to their higher rates of speciation and extinction, the clades will present an overrepresentation of biome specialists (i.e. species restricted into a single biome) in relation to the proportion of generalists. The second premise states that due to its ecological features, certain clades will tend to be more specialist than others. This point was broadly consistent with our findings. Faunivorous clades were more generalist than herbivorous clades. Omnivores showed an intermediate position. Likewise, migratory behaviour showed to be an important adaptive strategy that allowed the occupation and diversification of many lineages in hostile environments and, against initial assumptions, did not affect overall

trends of biome specialization. Finally, the third premise establishes that there will be a prevalence of specialist species in the tropical rainforest, desert, steppe and tundra biomes. These environments are extremes of the climate gradient are highly susceptible to the fragmentation and reduction-expansion processes during climate change periods. Therefore, these biomes constitute important scenarios of speciation and extinction in bird lineages. Although not contemplated within the hypothesis premises, we obtained important evidences of influence of biome specialization due to altitudinal gradients in the tropic highlands, heterogeneity of habitat and biotic interchanges events during the Neogene on the macroevolution patterns of non-passerine birds.

According with the chapter 3, based in the phylogenetic relationships of all living birds and their best-known fossil relatives, we assessed different biogeographic scenarios for the evolution of birds. The implemented analysis considers all palaeogeographic evidence of tectonic and climatic changes on Earth along the evolution of modern birds. In this context, the flight and its different variations have been key to evolutionary success of birds. Respect to this, we established statistically the most probable biogeographic scenario for all bird high-clades and for Neornithes using maximum likelihood criteria. Our methodology allowed us integrating geographic, historical fossil and recent information.

Our findings suggest that early evolution of the first Neornithes took place in South America. This continent would have played a key role as a refuge in periods of major environmental change during the latest Cretaceous, which caused the extinction of other vertebrate lineages. Over the evolutionary history of Neornithes, diverse dispersal and colonization events have been fundamental for subsequent vicariance episodes and diversification within bird lineages. Diverse moments of dispersion events would configure the macroevolutionary patterns of birds. The first one, during the late Upper Cretaceous where the ancestors of land-cursorial and aquatic lineages Paleognathae, Galloanseres and Aequornithes disperse from South America to Africa, Antarctica and North America. Likewise, a second wave of diversification would have occurred along the late Paleocene and early Eocene. This event allowed the diversification of bird families with tree-dwelling habits and prominent fly capacity as diverse lineages within Caprimulgiformes and Afroaves. The patterns obtained suggest

a possible relationship between these processes and the expansion of tropical ecosystems at high latitudes during this period. Later, during the Oligocene, significant global changes conditioned the appearance of novel seasonal and open biomes due to global cooling trends. According to the above, our results suggest that the emergency of these new niches promoted a new pulse of dispersion in marine and land-cursorial lineages. During this period, diverse shorebirds and seabirds (Procellariiformes and Charadriiformes) and modern lineages of fowls (Galliformes), bustards (Otidiformes) and other lineages adapted to open environments showing a prominent diversification. Finally, during the Miocene and Pliocene, with the intensification of seasonal patterns in the Northern Hemisphere, important retraction events in tropical forests towards equatorial latitudes caused the extinction of many bird families in emerging seasonal temperate environments, which confined their distributions to Panropical biomes.

The chapter 4 explores the historical process of biome occupation considering a phylogenetic perspective. This allowed integrating evolutionary hypotheses as niche conservatism into the biome historical dynamics. As we highlight in Chapter 2, the biomes are consolidated as key ecological units for macroevolution and macroecological studies, due to their structure and history, which is closely connected to climatic variables and geological processes. In addition, the implicit phylogenetic signal in the taxa provides the opportunity to study the influence of biome dynamics and the processes of adaptation to climate regimes under deep-time perspective. For this, we used recently-developed analytical techniques based on phylogenetic information to reconstruct the historical occupation of climatic "evolutionary arenas".

Galliformes and Falconiformes are distributed worldwide. Moreover, these groups have evolved adaptations linked to their different trophic strategies: herbivores and faunivores respectively. The extensive knowledge of their phylogenetic relationships at the species-level and the vast ecological information available allowed us to study their historical dynamics in biome occupancy. In this way, we aimed to clarify what environmental factors were critical in this occupation patterns and what are the main trends in the evolution of the climate niche by assessing the phylogenetic conservatism at the scale of biomes.

Finally, the results of this chapter are broadly consistent with phylogenetic niche conservatism in both groups. The biome conservatism was particularly marked in

biomes of extreme conditions within the climatic gradient. Thus the findings reflect the development of specific morphological and physiological features to colonize these environments, which tend to constrain subsequent colonization events. Similarly, our findings suggest that the different climate changes occurred during the Miocene triggered the main diversification pulses in both groups. During this period, the adaptation and wide occupancy of seasonal dry biomes such as tropical dry forest and savanna would have allowed the subsequent colonization of other biomes, in tropical and temperate latitudes. The findings suggest the important role as “species source” of the tropical deciduous woodland, which consolidate this biome as important player in diversification processes.

Conclusions

Overall, our results provide a holistic view of the important role played by global climate changes and tectonic processes in structuring living non-passerine birds diversity and disparity. Our approach shows the great importance of the study of modern faunas and their phylogenetic relationships to obtain evolutionary inferences of high explanatory power. Finally, this study opens a new perspective that integrates neontological and paleontological data in a historical context for understanding and shed valuable light about the complex evolutionary process of modern birds lineages since their origin until our days.

1

Introducción





Introducción

1

"Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends"

Charles Darwin (1845)

"New evolution research ruffles some feathers"

Mark Norrell (1996)

Desde su origen en el Jurásico Superior las aves se han diversificado exitosamente logrando colonizar todos los ambientes del planeta Tierra (Cracraft 1986; Padian & Chiappe 1998; Chiappe & Witmer 2002; Del Hoyo et al. 1992-2002; Jetz et al. 2012). A lo largo de su historia han desarrollado una gran variedad de adaptaciones que les ha permitido ocupar nichos ecológicos de diverso tipo; desde polinizadoras como los colibríes, dispersoras de semillas como las palomas, pasando por especies ictiófagas, insectívoras e incluso carroñeras. Muchos de estos nichos han permitido a las aves un papel fundamental en numerosas relaciones de coevolución con otras especies en los ecosistemas, como en el caso de diversas especies polinizadoras y dispersoras de semillas que se han diversificado a partir de la evolución paralela ave-planta en ambientes tropicales (Wheelwright 1985; Gill 2007;

1. Introducción

Cronk & Ojeda 2008; Pettingill 2013). Con cerca de 10000 especies, la diversidad de las aves en la actualidad es muestra de su destacado éxito evolutivo entre los vertebrados, y sin lugar a dudas esta predominancia ecológica es debida en gran medida al desarrollo de la capacidad voladora (Ksepka 2014). Asimismo, características como sus hábitos principalmente diurnos, ser frecuentes y activos voladores en muchos ecosistemas, así como su estética llamativa fueron factores decisivos que consolidaron a las aves como objeto de estudio preferente por los primeros naturalistas, que se maravillaron con la investigación de todo lo que las rodeaba (Audubon 1843; Birkhead & Charmantier 2001; Egerton 2003; Haffer 2008). De esta manera, las aves han llegado posiblemente a ser el grupo de vertebrados mejor estudiado en términos de su ecología, comportamiento y distribución geográfica.

1. El estudio de la evolución en las aves.

Desde las descripciones de Linneo, pasando por los estudios de Humboldt en Sudamérica o Wallace en el Sudeste Asiático, hasta los míticos pinzones de Darwin (Birkhead & Charmantier 2001), las aves históricamente se han convertido en un grupo modelo para el estudio de diversos procesos evolutivos (Mayr 1940; Cracraft 1985a; McKittrick & Zink 1988; Block & Brennan 1993; Fjeldså 1994; Holmes & Austad 1995; Gottschalk et al. 2005; Grant & Grant 2006; Cardillo et al. 2005; Chesser & Zink 1994; Jetz et al. 2008; Phillimore et al. 2008; Lanfear et al. 2010). Muchos estudios se realizaron en el pasado y también en la actualidad acerca de sus dinámicas ecológicas, patrones de migración, variación intraespecífica y genética poblacional, así como de los patrones de especiación y extinción, relaciones filogenéticas, entre otros muchos aspectos de su biología (Martin 1995; Marshall 2013; Schreiber and Burger 2001; Newton 2003; Berthold et al. 2003; Jetz et al. 2012; Jarvis et al. 2014). Sin embargo, desde el punto de vista de los estudios de la paleontología de las aves, algunos de los principales avances son relativamente recientes, la gran mayoría de ellos de los últimos 20 años (Gauthier and Gall 2001; Chiappe and Witmer 2002; Mlíkovský 2002; Mayr 2009; O'Connor and Zhou 2013; Lee et al. 2014). Durante décadas los únicos conocimientos destacados sobre la paleontología y las relaciones filogenéticas de las aves fueron los referentes a su ancestro *Archaeopteryx lithographica* (Heilmann 1926; Ostrom 1974, 1976) o a los

hallazgos y estudios de aves mesozoicas como *Ichthyornis* y *Hesperornis* hechos en Norteamérica (Gregory 1952; Gingerich 1972; Gingerich 1973).

La historia de *Archaeopteryx* comienza a mediados del siglo XIX cuando Richard Owen realiza la descripción (Owen 1863) del que sería históricamente fundamental en el respaldo de la misma teoría evolutiva (Darwin & Wallace 1858) y por mucho tiempo el icono de la evolución. Aunque adecuadamente clasificado por Owen como un ave, tendría que llegar Thomas H. Huxley para que tras un estudio detallado se planteara su naturaleza “reptiliana” (Huxley 1868). Con esta evidencia de ancestría para las aves, Huxley se dio a la tarea de encontrar “parentescos” comparando diversos reptiles mesozoicos encontrados hasta ese momento. Él identificaría importantes similitudes anatómicas entre el terópodo *Compsognathus* y *Archaeopteryx* (Huxley 1870). Esta comparación sería revolucionaria para la época y fundamental para posteriores estudios morfológicos (Chiappe & Witmer 2002; Mayr et al. 2005).

La idea del origen dinosauriano de las aves quedaría relativamente rezagada a consecuencia de los estudios de Heilmann (1926) e incluso por el mismo Huxley (1870), quienes no apoyarían la descendencia terópoda de las aves debido a la ausencia de clavículas en los terópodos y la presencia de las mismas a modo de fúrcula en las aves. De esta manera, por mucho tiempo se consideró un origen a partir de grupos basales de reptiles diápsidos (origen tecodonto). Sin embargo, la visión de las aves como dinosaurios seguiría latente desde Huxley y sería posteriormente retomada por algunos investigadores a la luz de nuevos descubrimientos. En la década de los 70 las comparaciones anatómicas que realizó Ostrom (1976) con el recientemente descrito dinosaurio *Deinonychus* pondrían de manifiesto de nuevo muchas similitudes morfológicas entre estos terópodos y las aves. Asimismo, posteriormente se realizarían hallazgos de numerosos dinosaurios terópodos que aportaron nueva información morfológica y arrojarían mayor luz al estudio de las relaciones evolutivas existentes entre terópodos y sus descendientes actuales, las aves (Ostrom 1976; Qiang et al. 1998; Sereno 1999; Chiappe & Witmer 2002; Göhlich & Chiappe 2006; Zhang et al. 2008).

En los últimos años, importantes evidencias han logrado aportar indicios acerca del desarrollo de las características que definen típicamente a las aves, como es el caso del plumaje (Prum & Brush 2002; Longrich 2006; Zelenitsky et al. 2012; Clarke 2013; Zheng et al. 2013; Foth et al. 2014; Zhou 2014; Feo et al. 2015). Este

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carácter actualmente es considerado como plesiomórfico dado su registro para diversos dinosaurios terópodos en los que se han encontrado desde estructuras filamentosas similares a la filopluma hasta incluso plumas en el sentido moderno estructuralmente hablando (Norell et al. 2002; Xu et al. 2009; Xu et al. 2010; Clarke 2013; Foth et al. 2014). Estos hallazgos integrados a nuevos análisis filogenéticos han llevado a relacionar aves con los linajes terópodos dromaeosauridos y troodontidos (Foth et al. 2014). En la medida que más caracteres se suman como plesiomorfías de las aves con respecto a sus ancestros (O'Connor & Claessens 2005; Salvador & Fiorelli 2011; Benson et al. 2014), resulta incuestionable el replanteamiento de la monofilia tradicional e histórica del grupo. Considerando lo anterior, (Chiappe 2002) define tres sinapomorfías para las aves: 1) El margen posterior de foramen nasal llega o se superpone al borde anterior de la fosa anteorbital; 2) La escápula presenta un acromion destacado, y 3) El proceso postacetabular es poco profundo y puntiagudo, menos del 50% de la profundidad del ala preacetabular. Queda así definido el clado Avialae como aquel que incluye a *Archaeopteryx* y a todos sus descendientes (Turner et al. 2012).

1.1. *Archaeopteryx* y la diversificación de sus descendientes durante el Mesozoico

Filogenéticamente las aves son dinosaurios terópodos, y *Archaeopteryx*, además de ser un icono de la paleontología por el excepcional estado de preservación de sus 12 especímenes (Mayr et al. 2007; Callaway 2014; Foth et al. 2014), ha conservado por cerca de 150 años su posición de “primer ave”, la cual ha sido cuestionada por hallazgos recientes como el de *Aurornis xui* en China (Godefroit et al. 2013; Callaway 2014). Sin embargo, y aunque *Archeopteryx* sea relevado por futuros hallazgos, durante muchos años el análisis de sus fósiles ha aportado una valiosa información sobre los procesos evolutivos durante la transición dinosaurio-ave (Brusatte et al. 2014; Callaway 2014; Foth et al. 2014; Ksepka 2014). Por tanto, su estudio seguirá siendo fundamental para comprender los procesos de cambio morfológico y adaptativo que llevaron a las aves a consolidarse en lo que son actualmente. De esta manera, ha sido posible obtener un amplio abanico de información anatómica que ha permitido realizar análisis filogenéticos entre *Archaeopteryx* y el creciente número de formas Mesozoicas que han hecho su aparición en el registro fósil como *Jeholornis* o

Confuciusornis (Chiappe et al. 1999; Zhou & Zhang 2003), presentando una condición relativamente basal en comparación a otros linajes más derivados como *Enanthiornithes* y *Ornithurines* (Chiappe & Witmer 2002; O'Connor & Chiappe 2011; Lee et al. 2014).

Una de las características más notorias de *Archaeopteryx* es su plumaje, el cual se caracteriza por una organización estructuralmente similar a la observada en las aves modernas, con un raquis y un véxilo asimétrico. Al igual que en las aves actuales presenta de 11 a 12 plumas primarias y de 12 a 15 secundarias (Elzanowski 2002). La presencia de estos caracteres ha hecho que la capacidad voladora de *Archaeopteryx* sea tema de debate y diversos estudios (Chatterjee & Templin 2003; Burnham 2007; Foth et al. 2014). Sin embargo, parece claro que el análisis de muchas características anatómicas son un componente clave para estudiar el origen del vuelo (Pelegrin 2010). Mientras que algunos autores debaten si la articulación de sus alas les habría permitido batirlas por encima del cuerpo (Senter 2006), diversos análisis de su posible capacidad pulmonar (Christiansen & Bonde 2000; O'Connor & Claessens 2005), metabolismo a partir de estructura esquelética (Erickson et al. 2009) y estructura neurosensorial (Alonso et al. 2004) sugieren una destacada capacidad voladora. Por otra parte, también se ha sugerido que los ancestros de *Archeopteryx* eran un animales predominantemente terrestres y que el vuelo habría surgido desde el suelo a partir de una actividad corredora. Frente a esto, Mayr (Mayr et al. 2005) reporta que el hallux de *Archaeopteryx* esta orientado de forma distinta respecto a especies arborícolas, lo que implicaría una forma de vida terrestre. Por el contrario, autores como Feduccia (1999) analizando la curvatura de las garras propone un contexto arbóreo para la evolución del vuelo (Chatterjee & Templin 2003; Burnham 2007).

El hallazgo de dinosaurios maniraptores (*Microraptor gui*) con plumaje desarrollado y posiblemente apto para el vuelo en las extremidades posteriores (Xu et al. 2003; Xu and Zhang 2005; Chatterjee & Templin 2007; Zheng et al. 2013) así como nuevos análisis de *Archaeopteryx* (Longrich 2006; Foth et al. 2014) y otras aves mesozoicas (e.g. *Sapeornis*) han permitido proponer un escenario en donde el vuelo surge a partir de dinosaurios planeadores y con una destacada vida arborícola y una condición “tetralar” (Longrich 2006; Chatterjee & Templin 2007; O'Connor et al. 2011). Posteriormente con el desarrollo del vuelo activo en el linaje de *Archaeopteryx*,

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el plumaje de las patas posteriores habría sufrido una reducción considerable hasta consolidarse evolutivamente la condición bialar (Longrich 2006; Zheng et al. 2013). Finalmente, a la luz de las actuales evidencias, parece razonable afirmar que la evolución del vuelo en las aves tiende aún más a explicarse estableciendo matices adaptativos y no un simple juego de hipótesis dicotómicas.

En los últimos años el registro fósil de las aves de periodos mesozoicos ha sufrido un aumento considerable (Chiappe & Dyke 2002). Grupos como Enantiornithes, de importante presencia durante el Cretácico, han sido encontrados en Argentina, España y especialmente China (Chiappe 1995; Sanz et al. 1996; Chiappe & Witmer 2002; Sanz & Ortega 2002; Zhou & Zhang 2007; Li et al. 2010), evidenciando así el alto grado de dispersión que alcanzaron las primeras aves. Diversos descubrimientos han logrado aportar importantes datos sobre la evolución de la morfología, la dieta e incluso lograr inferir posibles rasgos comportamentales de muchas especies extintas de aves (Zhou & Zhang 2007; Li et al. 2010; Naish 2014; Pelegrin et al. 2014b). De esta manera se ha mejorado sustancialmente el conocimiento de la inicial diversificación de las aves y su relación con la adquisición de ciertos caracteres anatómicos e innovaciones evolutivas que serían fundamentales en el éxito ecológico de las aves modernas.

1.1.1. *Ornithothoraces: Enantiornithes*

Ornithothoraces hace referencia al clado que incluye a los ancestros de Enantiornithes y Euornithes y a todos sus descendientes (Fig.1). En este linaje se evidencia una mayor tendencia hacia la fusión esquelética con el desarrollo del tarsometatarso y carpometacarpo, así como la modificación estructural del esternón y la presencia del álula lo que sugiere un vuelo mucho más activo en estos linajes que en sus contrapartes más primitivas. Enantiornithes (*Aves opuestas*) recibe su nombre por la condición contraria presente en la articulación del coracoides y el esternón en la cintura escapular respecto a las Euornithes (Walker 1981), en estas últimas la escapula presenta una prominencia que se ajusta al coracoides, condición que es contraria en los Enantiornithes, en los cuales se articula el coracoides con la escapula (Chiappe et al. 2002). Su estructura craneal presenta caracteres relacionados con la poca fusión ósea como la presencia de un hueso postorbital o la conservación de un dentario no bifurcado (O'Connor & Chiappe 2011). Asimismo, poseen una

estructura premaxilar y maxilar con dientes, concentrados en muchas especies en los extremos de la boca (Louchart & Viriot 2011; Turner et al. 2012).

Con cerca de 60 especies descritas, Enantiornithes posiblemente fue el grupo de aves más exitoso durante el Cretácico con respecto a las primeras Euornithes (Longrich et al. 2011) y ocuparon todos los continentes exceptuando la Antártida (Chiappe et al. 2002; O'Connor 2009). Pese a su relativa uniformidad anatómica, esta amplia distribución geográfica da idea de su grado de dispersión lo que ha llevado a muchos autores a compararlas con las actuales passeriformes (Chiappe & Dyke 2002; Chiappe 2007; O'Connor et al. 2013). Sin embargo otros autores sugieren que su disparidad ecológica pudo estar inicialmente restringida por los pterosaurios, reduciendo posiblemente su presencia a ciertos ambientes y ecoespacios, lo cual sería consistente con una radiación inicial durante el Cretácico en algunos nichos específicos, pero no muy diversos en comparación a los que llenarían los representantes de Euornithes (específicamente Neornithes) durante el Cenozoico (Mitchell & Makovicky 2014).

Características anatómicas como la presencia de hallux oponible, la retención de garras en las extremidades anteriores así como hallazgos que han permitido inferir su dieta, han sugerido que los Enantiornithes eran principalmente aves de hábitos terrestres dominantes en ambientes forestales donde presentarían una amplia gama de hábitos alimenticios que irían desde partes blandas de vegetales como en *Pengornis houi* (O'Connor & Chiappe 2011) o insectos como *Sulcavis geeorum* (O'Connor et al. 2013). Igualmente, parece ser que algunos linajes pudieran haberse especializado en ser rapaces (i.e. *Bohaiornis*) o en la captura de peces en ambientes lacustres (i.e. *Longipteryx chaoyangensis*) (Hou et al. 2004; Li et al. 2014; Wang et al. 2014). Esto las convertiría en importantes componentes de los ecosistemas cretácicos hasta su extinción en el evento Cretácico/Paleógeno (Longrich et al. 2011).

1.1.2. Euornithes = Ornithuromorpha

Este clado engloba a todos los linajes de aves más cercanas a las actuales Neornithes que Enantiornithes (Turner et al. 2012). Una de las principales innovaciones evolutivas que presentan las primeras Euornithes es un mayor estado de reducción y modificación del pigóstilo que les permitiría una cola con plumaje en

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forma de abanico (Fig.1). Esta estructura sería bastante similar respecto a las formas modernas (Neornithes), representando una importante ventaja adaptativa en términos de maniobrabilidad durante el vuelo (Martyniuk 2012; O'Connor & Zhou 2013). A diferencia de Enantiornithes, Euornithes desarrolla una estructura de pico homologa a la de Neornithes. Sin embargo, al igual que en muchos linajes basales de Avialae se presenta una importante retención de dientes en las mandíbulas y por consiguiente, el desarrollo del pico estará restringido a la región más distal de las mandíbulas (Zhou & Zhang 2006). Esta condición dentada en las formas más basales de Euornithes estará asociada al hueso prementario en la mandíbula inferior y será perdida completamente en las aves modernas (Louchart & Viriot 2011; Meredith et al. 2014).

El análisis ecológico de la abundancia y estructura anatómica de los primeros Euornithes ha llevado a sugerir un modo de vida acuático como condición ancestral para este grupo, esto se ha evidenciado en la asociación de muchos de los ejemplares encontrados con ambientes acuáticos del pasado (Longrich 2009). Igualmente, dada la presencia de mandíbulas predominantemente dentadas de estas formas, asociándolas con la captura de peces e invertebrados o el hallazgo de ejemplares con adaptaciones especializadas a modo de lamelas para dietas más herbívoras (Zhou & Zhang 2005, 2006). Esto ha permitido plantear un escenario en donde los linajes de Enantiornithes habrían sido abundantes en los ambientes continentales, mientras que los de Euornithes por su parte habrían estado asociados a ambientes acuáticos (Longrich 2009; You et al. 2006; Wang et al. 2015).

1.1.3. Euornithes derivados: Ornithurae

Ornithurae es un clado que contiene a *Gansus* y todos sus descendientes (Dalsätt 2012), estos linajes estarían más próximos a Hesperornithiformes y al clado Carinatae (Fig.1), este último conformado por el linaje de las aves Ichthyornithes y el de las aves Neornithes como grupos hermanos (Turner et al. 2012). El establecimiento monofilético de Ornithurae esta sustentado por diversas sinapomorfías como: disminución en el número de vertebras torácicas y fusión de vertebras sacras formando el sinsacro; pubis e isquion más o menos paralelos y dirigidos posteriormente; reducción del acetábulo; diversos caracteres asociados a los metatarsos; y un destacado ensanchamiento del esternón para el posterior desarrollo

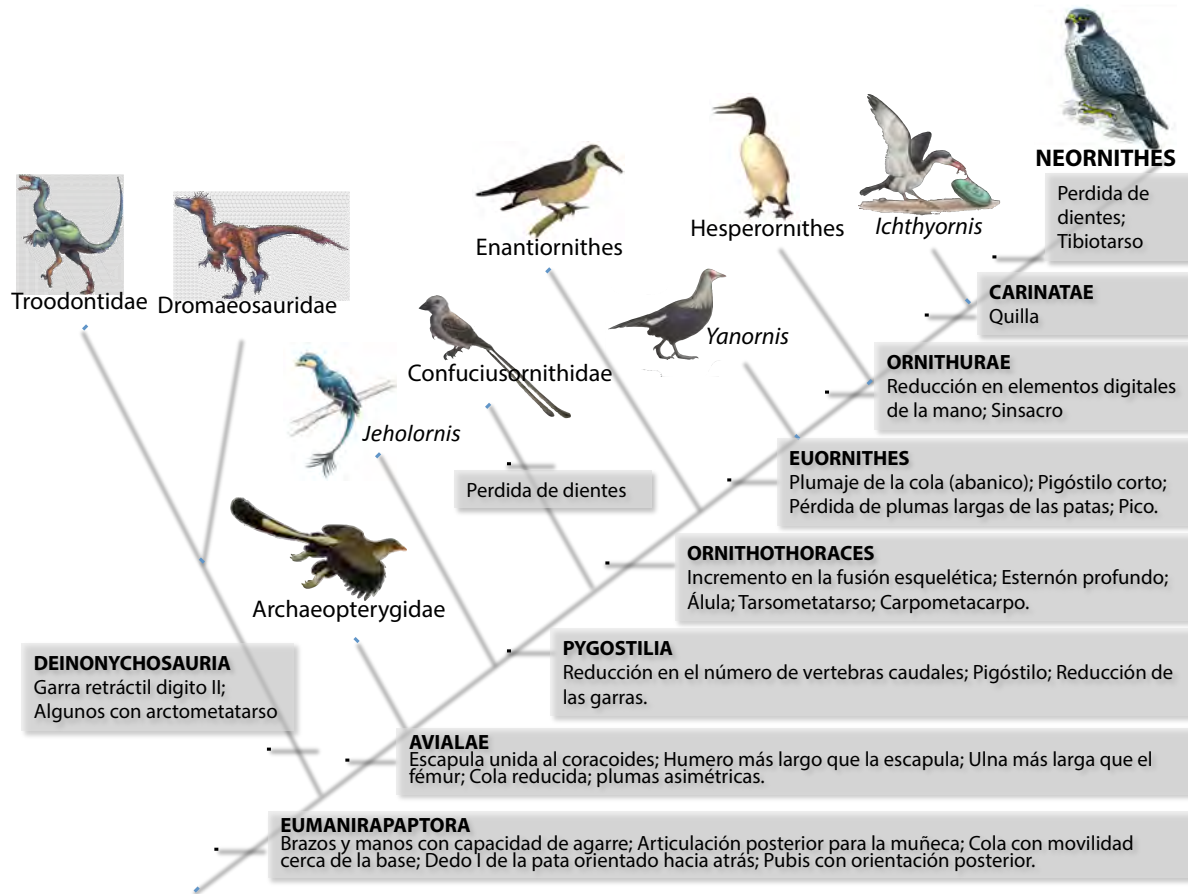


Figura 1. Principales clados de aves y sus sinapomorfías más relevantes.

de una quilla para inserción muscular. Este último rasgo anatómico sería definitorio del clado Carinatae, en dónde sería mucho más destacado dada su importancia funcional. Asimismo este linaje desarrollaría otras innovaciones evolutivas que se pueden apreciar en las aves actuales como lo son el desarrollo de un cráneo globoso o la fusión metacarpal completa (Chiappe & Dyke 2002; Dalsätt 2012).

La gran mayoría de los miembros cretácicos de Ornithurae serían formas predominantemente acuáticas (Longrich 2009; Wang et al. 2015). *Gansus yumenensis* del Cretácico Inferior (115 – 105 Millones de años), uno de los miembros más antiguos del clado, posee características anatómicas que sugieren una capacidad natatoria que semejarían funcionalmente a los zampullines actuales (You et al. 2006; Dalsätt 2012; Wang et al. 2015). Por otra parte, los Hesperornithiformes con cerca de 20 especies descritas y una distribución geográfica restringida al Hemisferio Norte durante el Cretácico Superior, representan el primer grupo de aves en el registro fósil

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con una morfología fuertemente hidrodinámica. Esto ha sugerido una evolución de este linaje en estrecha asociación con una vida acuática estricta, similar a los actuales colimbos (Martin 1984; Rees & Lindgren 2005; Bell & Everhart 2009; Wilson et al. 2011).

Dentro del clado Carinatae, el linaje Ichthyornithiformes estuvo representado por especies de una morfología similar a la que podría encontrarse en las gaviotas actuales, esto ha sugerido una ecología y hábitos convergentes (Clarke 2004). *Ichthyornis* y otras especies habrían tenido una destacada presencia en los ecosistemas costeros y marinos del Cretácico Superior donde se habrían alimentado de peces e invertebrados (Chiappe & Witmer 2002; Clarke 2004; Dalsätt 2012). A pesar de la presencia de dientes (Martin & Stewart 1977), podría decirse que su anatomía era prácticamente moderna y habría sido probablemente una especie con una capacidad voladora altamente desarrollada (Clarke 2004).

1.2. Neornithes: Las aves modernas

1.2.1 Los Neornithes durante el Cretácico

Neornithes representa el clado que incluye por los linajes del “crown group” Avialae que viven en la actualidad y sus parientes más próximos extintos durante el Cenozoico (Mayr 2009). Se caracterizan fundamentalmente por cerca de 11 sinapomorfias craneales y poscraneales, algunas de las cuales son: la pérdida completa de los dientes, la presencia de un coracoides neummatizado o el desarrollo de un tibiotarso (Turner et al. 2012). En términos de su registro fósil, los hallazgos de Neornithes durante el Cretácico Superior son escasos, limitados a pocos elementos anatómicos o compuestos por restos fragmentarios que no han permitido una fiable reconstrucción de su posible apariencia o establecer hipótesis sobre las relaciones filogenéticas de estos ejemplares con respecto a los linajes de Neornithes conocidos (Hope 2002; Chiappe & Dyke 2006). Pese a esta relativa poca abundancia, algunos de los especímenes encontrados han sido tentativamente asignados a grupos presentes en la actualidad, como el caso de *Vegavis* y *Presbyornis* emparentados con los Anseriformes (Livezey 1997; Clarke et al. 2005), *Austinornis* con los Galliformes o *Polarornis* posiblemente miembro del linaje Gaviiformes (Mayr 2009, 2014).

A partir del Paleoceno el registro fósil de Neornithes aumenta considerablemente (Olson 1985; Mayr 2009), planteando una amplia discusión relacionada con el *tempo y modo* de su diversificación y radiación adaptativa (Chiappe & Dyke 2006; Ericson 2008; Padian & de Ricqlès 2009). Bajo este contexto se han formulado dos hipótesis fundamentales. Por un lado, existe un punto de vista según el cual los linajes basales de Neornithes habrían sobrevivido a la crisis de finales del Cretácico para dar origen a una radiación adaptativa rápida a inicios del Paleogeno (Feduccia 1999; Feduccia 2003). Estos linajes de aves basales estarían representados por especies de aves adaptadas a ambientes costeros (Feduccia 2003). Por otra parte, diversos autores argumentan que los ancestros de los principales clados modernos habrían tenido su origen ya en el Cretácico Superior (Cooper & Penny 1997; Chiappe & Dyke 2006; Penny & Phillips 2004; Longrich et al. 2011). Con respecto a lo planteado, es importante anotar que tanto la evidencia fósil (Lee et al. 2014; Mayr 2014) como los más recientes estudios moleculares (Ericson et al. 2006; Hackett et al. 2008; Pacheco et al. 2011; Jarvis et al. 2014), establecen un origen para los grupos modernos de Neornithes en el Cretácico. De esta manera es posible generar una explicación que contraste las hipótesis en un escenario evolutivo en el cual probablemente los linajes de Neornithes mantendrían niveles bajos de diversidad a finales del Mesozoico por la competencia interespecífica con otros linajes de Ornithurae e incluso de Enantiornithes, Theropoda y Pterosauria (Cooper & Fortey 1998). Igualmente, algunos autores sostienen que la evolución inicial de Neornithes pudo darse en el Hemisferio Sur, esto explicaría la poca abundancia en el registro cretácico debido a importante sesgo de muestreo. Asimismo, el proceso de evolución inicial de Neornithes habría estado potenciado por el proceso de fragmentación de Gondwana durante el Cretácico, con una posterior colonización del Hemisferio Norte durante el Paleógeno (Cooper & Fortey 1998; Cracraft 2001; Ericson et al. 2002; Ericson 2012).

1.2.2. Relaciones filogenéticas de las aves modernas

Desde Linneo, la sistemática y el posterior estudio de la evolución de las aves se basó en su similitud morfológica, de esta manera se llegaron a consolidar grupos (órdenes y familias) establecidos a partir de caracteres relacionados con la estructura del pico, las proporciones de las extremidades o la configuración y disposición de los

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dedos en las patas (Birkhead & Charmantier 2001; Gill 2007). Con la introducción de las técnicas de análisis filogenético por similitud genética se presentó la oportunidad de conocer las relaciones evolutivas de las aves más allá de su morfología, la cual en muchos casos es el resultado de procesos de convergencia evolutiva (van Tuinen et al. 2001; Ericson 2012). Los estudios sistemáticos a partir de la hibridación del ADN realizados por Sibley y Ahlquist serían pioneros en la inclusión de datos moleculares para la inferencia de las relaciones filogenéticas en las aves a una gran escala taxonómica (Sibley & Ahlquist 1983; Sibley et al. 1988; Sibley & Ahlquist 1990). Estos análisis plantearían nuevos retos a la sistemática tradicional y abrirían toda una línea de investigación hacia análisis cada vez más complejos y con un mayor grado de resolución.

Los resultados de los análisis moleculares presentan una alta fiabilidad dada la independencia de la información de partida, como es el caso de los realizados a partir de ADN mitocondrial y nuclear (Houde 1987; Groth & Barrowclough 1999; Braun & Kimball 2002; García-Moreno et al. 2003; García-Moreno 2004; van Tuinen et al. 2004). Durante los últimos años una gran variedad de estudios moleculares han contribuido a esclarecer las relaciones evolutivas, así como a aportar indicios acerca del posible origen y radiación de los grandes grupos de aves (van Tuinen et al. 1998; Härlid & Arnason 1999; van Tuinen et al. 2000; Haddrath & Baker 2001; Barker et al. 2002; Paton et al. 2002; Fain & Houde 2004; van Tuinen et al. 2004; Pereira et al. 2007). Sin embargo, a pesar de la gran importancia de los estudios moleculares sólo en tiempos recientes se ha incluido información proveniente del registro fósil, la cual implica una integración entre la morfología y la información molecular (Ericson et al. 2006). El estudio morfológico permite establecer la relación evolutiva del espécimen fósil (Mayr 2014), y a su vez, sólo la información fósil puede proporcionar un marco temporal a las filogenias moleculares (van Tuinen & Hedges 2001; Ksepka et al. 2014; Mayr 2014).

A partir de los estudios moleculares se han consolidado tres grandes clados dentro de Neornithes. La divergencia inicial se presenta entre el linaje Paleognathae, representado por ratites y tinamúes, y el linaje Neognathae con los demás grupos de aves modernos (van Tuinen et al. 1998; Härlid & Arnason 1999; Hackett et al. 2008; Harshman et al. 2008; Baker et al. 2014). Este último a su vez estaría compuesto por los clados Galloanserae (gallinas, patos y afines) y Neoaves, que incluiría a la gran

mayoría de grupos actuales (Fig.2). Las relaciones filogenéticas de estos clados basales serían consistentes con las obtenidas en estudios morfológicos (Mayr & Clarke 2003; Mayr 2007; Livezey & Zusi 2007). Las discrepancias entre los diversos tipos de estudios se han presentado cuando se han realizado análisis filogenéticos morfológicos que pretenden analizar las relaciones evolutivas a gran escala y con una extensiva cantidad de caracteres. Sin embargo, pese a la poca consistencia de muchos de ellos con respecto a las propuestas moleculares, estos análisis han sido fundamentales para establecer sinapomorfias en los diversos clados que permiten una mejor identificación de los fósiles y su correcta asignación sistemática (Mayr 2007,2009, 2014).

Mientras las relaciones basales de Neornithes están relativamente bien establecidas, la sistemática de Neoaves ha sido materia de amplia discusión. Con numerosos análisis e intentos de resolver estas relaciones se estableció una divergencia de Neoaves en “Coronaves” y “Metaves” (Fain & Houde 2004). Sin embargo, dado que fueron realizados con un único marcador molecular, estos estudios fueron ampliamente cuestionados por su bajo nivel de confianza (Ericson 2008). Posteriormente se realizarían análisis considerando más datos moleculares y además integrarían esta información con fósiles para construir una propuesta consensuada. Ericson et al. (2006) a partir de un estudio de cinco genes nucleares complementado con información fósil, sugieren una primera aproximación a las relaciones evolutivas de los principales grupos incluidos en Neoaves (Ericson et al. 2006). Posteriormente estos resultados serían respaldados en el análisis realizado por Hackett et al. (2008) para 19 *loci* independientes en 169 especies (Hackett et al. 2008). Ambos trabajos pondrían de manifiesto la condición polifilética de muchos linajes considerados tradicionalmente como monofiléticos, como en el caso de las aves rapaces diurnas, ahora en dos ordenes: Accipitriformes y Falconiformes, la condición anidada del grupo Apodiformes (vencejos y colibríes) dentro de lo que clásicamente fue considerado Caprimulgiformes (chotacabras) o la reestructuración de las relaciones entre los clados de aves acuáticas Ciconiformes (cigüeñas), Pelecaniformes (pelicanos y garzas) y el recién creado Suliformes (alcatraces y fragatas). Asimismo, estas investigaciones, como muchas anteriormente mencionadas respaldarían un origen Cretácico para los principales clados de Neornithes (van Tuinen & Hedges 2001; Ericson et al. 2006; Hackett et al. 2008; Pacheco et al. 2011; Lee et al. 2014).

1. Introducción

A lo largo de la última década se han publicado diversas propuestas filogenéticas que incluyen un número relativamente alto de especies para muchos grupos de aves; Galliformes y Anseriformes (Eo et al. 2009; Stein et al. 2015), Apodiformes (McGuire et al. 2014), Falconiformes (*sensu lato* Wink et al. 1998; Griffiths et al. 2004) y (*sensu stricto* Fuchs et al. 2015), Psittaciformes (Tavares et al. 2006; Schweizer et al. 2010), Piciformes (Webb & Moore 2005; Fuchs et al. 2006), Passeriformes (Barker et al. 2004; Jönsson & Fjeldså 2006), entre otros (Friesen & Anderson 1997; Thomas et al. 2004). La creciente cantidad de información filogenética dentro de los diversos grupos y los análisis a gran escala de Ericson et al. (2006) y Hackett et al. (2008), permitieron que Jetz et al. (2012) realizarían una propuesta filogenética con todas las especies de aves actuales analizando sus tasas de diversificación en el tiempo y el espacio. A pesar de constituirse como la primera gran aproximación hacia una visión filogenética general, esta no alcanzaría suficiente soporte estadístico en muchos de sus clados (Jetz et al. 2012).

Con un promedio de 1.45 miles de millones de pares de bases y siendo de los más pequeños entre los vertebrados, el genoma de las aves representa una importante fuente de información en términos de sus regiones no codificantes (Gregory 2002; Lanfear et al. 2010). Diversos estudios han sugerido que el tamaño del genoma se correlaciona con altas tasas metabólicas y que probablemente se presentó una destacada tendencia hacia su disminución en los linajes de dinosaurios saurisquios, especialmente en los linajes de terópodos carnívoros de los cuales las aves descienden (Organ et al. 2007; St John et al. 2012). Lo anterior revela la importancia que representa el análisis del genoma completo en el establecimiento de las relaciones evolutivas de las aves. Considerando esto, no sería hasta finales del año pasado cuando Jarvis et al. (2014) plantearían una filogenia que incluiría el análisis completo del genoma para 48 especies de aves, representando todos los principales grupos taxonómicos a escala de orden (Fig. 2). Con esta aproximación filogenética se logró consolidar lo propuesto en hipótesis anteriormente publicadas con respecto a ciertas relaciones basales, así como arrojar mayor luz sobre la resolución de diversas relaciones debatidas. Esta última propuesta ha sido la considerada como base filogenética para el desarrollo de este trabajo de Tesis Doctoral.

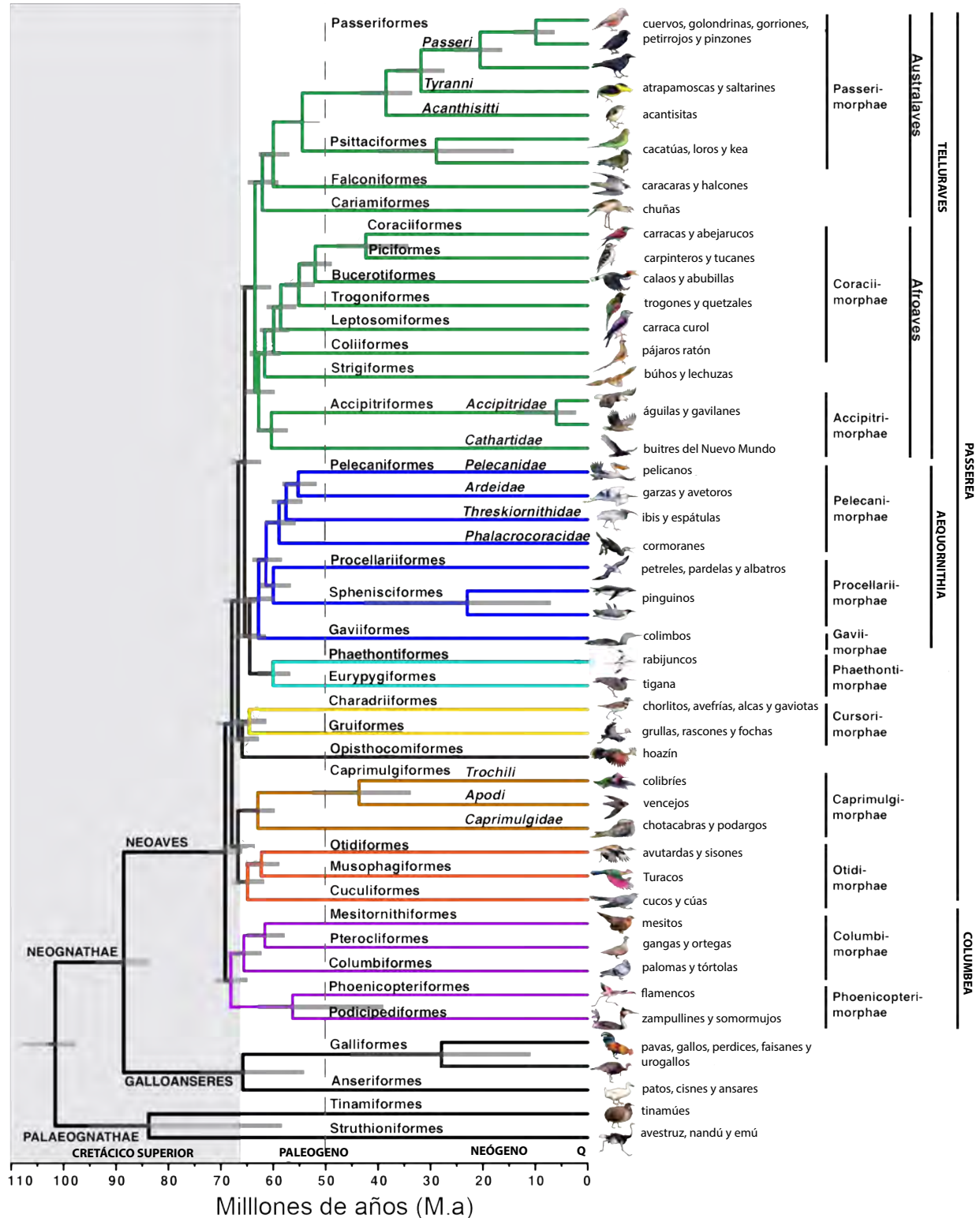


Figura 2. Propuesta filogenética de Jarvis *et al.* (2014) que resume los grupos de estudio de esta Tesis Doctoral y las relaciones evolutivas fundamentales consideradas para los diversos análisis. Q, Cuaternario. (Modificado de Jarvis *et al.* 2014).

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2. Contexto filogenético, ecológico y paleontológico en macroevolución.

Inspirados en la figura de G.G Simpson, durante la década de los 70 un creciente número de paleontólogos decidieron apuntar sus esfuerzos hacia el estudio de los procesos evolutivos, labor que hasta ese entonces era desarrollada por genetistas y ecólogos (Mayr 1940; Dobzhansky 1950; Fischer 1960). Esto implicaría el desarrollo de una amplia diversidad de líneas de investigación en la que sería llamada la revolución paleobiológica (Turner 2011). Autores como N. Eldredge, S.J. Gould, D. Raup, J. Sepkoski, S. Stanley y E.Vrba, entre otros, bajo la premisa que el estudio de los fósiles puede aportar invaluable información sobre los procesos evolutivos, realizarían importantes avances hacia la generación de nuevas hipótesis y teorías evolutivas a partir de información paleontológica (Raup et al. 1973; Stanley 1975; Gould & Eldredge 1977; Gould et al. 1977; Vrba 1980; Gould & Vrba 1982; Raup & Sepkoski 1986; Vrba & Gould 1986; Vrba 1992; Sepkoski Jr 1993, 1996). Este sería el comienzo de lo que se denominaría la escala macroevolutiva, la cual se define como el estudio de los cambios y procesos evolutivos por encima del nivel de especie (Stanley 1975; Cracraft 1985b). Uno de los procesos que más ha intrigado a los investigadores es el incremento en la biodiversidad y por qué ciertos taxones presentan una mayor riqueza de especies con respecto a otros (Gaston 2000).

Considerando lo anterior, el estudio de la diversificación como el balance de especiación y extinción es fundamental para comprender la dinámica de cómo los grupos han evolucionado hasta nuestros días (Mittelbach et al. 2007; Morlon 2014). A lo largo de la historia de la tierra factores abióticos como cambios climáticos y procesos geológicos han provocado la extinción de muchas especies e incluso de taxones completos (Sepkoski Jr 1996; Arens & West 2008; Benton 2009), así como también la posterior radiación adaptativa de otros (Cooper & Fortey 1998). Esto hace de los factores abióticos importantes condicionantes del componente biótico y por consiguiente principales promotores de cambio evolutivo a gran escala (Vrba 1993; Vrba 2004; Benton 2009; Condamine et al. 2013a).

En la visión clásica las primeras representaciones filogenéticas eran una mera esquematización de las relaciones de parentesco entre los grupos naturales y eran una importante herramienta en la clasificación taxonómica (Turner 2011). Sin embargo, en la actualidad con el desarrollo de técnicas moleculares y computacionales más eficientes, las aproximaciones filogenéticas son cada vez más robustas y confiables

permitiendo un mejor conocimiento de los patrones evolutivos de las especies (Glor 2010; FitzJohn 2012; Drummond et al. 2012; Pennell & Harmon 2013; Morlon 2014). El creciente surgimiento de filogenias con un mayor contenido de clados relacionados entre sí ha ofrecido una fuente de información a los estudios macroevolutivos para consolidar diversos métodos comparativos que integran las filogenias con gran cantidad de datos biológicos y paleobiológicos (Garland et al. 1993; Alroy 1996; Mooers et al. 1999; Losos & Glor 2003; Garland et al. 2005; Cardillo 2011; Eastman et al. 2011; Jetz et al. 2012; Pennell & Harmon 2013; Cantalapiedra et al. 2013; Cantalapiedra et al. 2014; Morlon 2014). Asimismo, debido a que su topología tiene implícita la señal del pasado, esto ha permitido ampliar el horizonte explicativo de la influencia de los procesos históricos, algunos de ellos bien conocidos, en la diversificación de los diversos grupos taxonómicos (Hawkins et al. 2006; Hernández Fernández & Vrba 2005b; Finarelli & Badgley 2010; Hoffmann & Sgrò 2011; Cantalapiedra et al. 2011; Kozak & Wiens 2012; Toussaint et al. 2012; Davies & Buckley 2011; Condamine et al. 2013b; Near et al. 2013; Batalha-Filho et al. 2014).

En este contexto y desde una perspectiva paleobiológica, la inclusión de información fósil provee un marco conceptual importante para el estudio de diversas hipótesis macroevolutivas a través de los patrones observados e inferidos en las filogenias (Gavrillets & Losos 2009; Pennell & Harmon 2013). Preguntas acerca de cómo han cambiado la disparidad y la diversidad a través del tiempo; cuáles han sido los principales agentes históricos (abióticos y bióticos) que han influido en estos patrones; cuáles han sido los roles de la dispersión y la vicarianza en los patrones biogeográficos de la diversidad, así como el papel de las innovaciones evolutivas en la diversificación, son preguntas que son abordadas con renovado entusiasmo gracias a la creciente información paleontológica y paleoecológica (Barnosky 2001; Sanmartín & Ronquist 2004; Noonan & Chippindale 2006; Hernández Fernández et al. 2007, 2015; Tiffney 2008; Davies et al. 2011; Pyron & Burbrink 2012; Tingley & Dubey 2012; Álvarez-Sierra et al. 2013; Gómez Cano et al. 2013, 2014; Benson et al. 2014; Domingo et al. 2014; Mitchell & Makovicky 2014; Pelegrin et al. 2014b; Morales et al. 2015). Los trabajos con información del registro fósil han resultado ser complementarios a las filogenias moleculares, aportando una evidencia histórica directa que permite la datación de las mismas mediante la asignación de un tiempo mínimo de ocurrencia de los eventos de cladogénesis (Hernández Fernández & Vrba

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2005b; Pennell & Harmon 2013; Mayr 2014). Asimismo, han logrado generar intervalos temporales para el desarrollo de determinados caracteres, algunos de ellos claves en los procesos de radiación adaptativa (Cantalapiedra et al. 2013; Pennell & Harmon 2013; Pelegrin et al. 2014b). Finalmente, los fósiles constituyen evidencias directas de presencia en un área geográfica determinada, que en muchos casos puede ser distinta a la actual (Mayr 2009). Este último aspecto es fundamental para el análisis espacio-temporal de la diversidad y en la reconstrucción paleobiogeográfica debido a que se pueden inferir las condiciones en las cuales habrían evolucionado los organismos en momentos tempranos de su historia (Maguire & Stigall 2008; Sanisidro & Cantalapiedra 2010; Loewen et al. 2013). En este sentido, con la integración de la biogeografía histórica, las distribuciones de los organismos en un contexto filogenético han aportado información acerca de la importancia de los procesos de especiación por dispersión o vicarianza en la diversificación de los linajes (Sanmartín & Ronquist 2004; Condamine et al. 2013b). Lo anterior ha sido fundamental para la generación de nuevas aproximaciones metodológicas integradas en análisis como Lagrange (Yu et al. 2015) o BioGeoBears (Matzke 2014), las cuales logran construir un modelo macroevolutivo de la dinámica espacio-temporal basado en datos filogenéticos, paleontológicos, geológicos y biogeográficos (Ree & Smith 2008; Alfaro et al. 2015; Mendoza et al. 2015).

En el caso de las aves, la información del registro fósil ha presentado un destacado incremento en las últimas décadas, y ha ofrecido la oportunidad de calibrar con mayor confianza las hipótesis filogenéticas más recientes (Ericson et al. 2006; Jetz et al. 2012; Jarvis et al. 2014). Sin embargo, muchas de las filogenias moleculares no consideran un número de fósiles adecuado o en muchos casos sus especímenes de referencia se corresponden con representantes de *stem groups* en lugar de *crown groups* lo que introduce un importante sesgo a las dataciones filogenéticas generando una sobre o subestimación del periodo de origen de los grupos (Ksepka et al. 2014; Mayr 2014). Aunque a diferencia de los mamíferos las aves no presentan un registro tan amplio (Alroy 2014), análisis como el de Ksepka y Boyd (2012) evidencian que este sí puede aportar evidencias históricas para la gran mayoría de los grupos presentes en la actualidad y muchos de sus parientes más próximos (Ksepka & Boyd 2012; Smith 2015).

La distribución geográfica de las especies actuales es el producto de su historia natural y esta en sí misma es una valiosa fuente de información para el estudio de los procesos evolutivos que han llevado a consolidarla (Vrba 1995; Cardillo 1999; Dynesius & Jansson 2000; Barnosky et al. 2003; Hawkins et al. 2003a; Gaston et al. 2004; Hawkins & Diniz-Filho 2004; Porzecanski & Cracraft 2005; Davies et al. 2011; Hernández Fernández 2001; Hernández Fernández & Vrba 2005a, 2005c, 2005d; Moreno Bofarull et al. 2008; Hawkins et al. 2012; Springer et al. 2012; Pigot & Tobias 2013; Cantalapiedra et al. 2014). En el caso específico de las aves, el destacado conocimiento de sus distribuciones y patrones migratorios (Del Hoyo et al. 1992-2002; Berthold et al. 2003), así como el creciente estudio de sus relaciones filogenéticas esta permitiendo el progresivo desarrollo de nuevas aproximaciones teóricas para establecer un marco espacial y temporal de cómo estos patrones se han configurado históricamente en las aves (Cracraft 1985a; Berthold 1999; Webb & Gaston 2000; Jetz & Rahbek 2002; Tris et al. 2004; Hawkins et al. 2006; Hawkins et al. 2007; Jetz et al. 2008; Şekercioğlu et al. 2008; Dalsgaard et al. 2011; Dalby et al. 2014; Kennedy et al. 2014; Rolland et al. 2014; Smith et al. 2014). Sin embargo, a diferencia de los trabajos con mamíferos, la inclusión de información fósil en este tipo de trabajos es aún escasa (García-R et al. 2014; Smith & Clarke 2014; Fuchs et al. 2015).

Desde una perspectiva ecológica, los ecosistemas están estructurados por un componente abiótico que a su vez condiciona el biótico (Brown 1995; Ricklefs 2008). De esta manera, las especies que componen la comunidad evolucionan con unas características particulares respondiendo así a las condiciones climáticas y ambientales del ecosistema (Newton 2003). Esto puede generar que aunque históricamente dos linajes sean distintos, su morfología y fisiología puedan ser similares (van Tuinen et al. 2001).

Existe un estrecho vínculo entre la evolución de los organismos y su contexto ambiental (Darwin 1859), así como regiones terrestres de mayor biodiversidad (Gaston 2000), y son muchas las hipótesis evolutivas que intentan explicar los patrones de distribución geográfica a la luz de la diversificación y distribución que muestran las especies (Mittelbach et al. 2007). Partiendo de la premisa de igual diversificación, autores pioneros como Wallace (1878) hasta modernos como Wiens & Donoghue (2004) o Fine & Ree (2006), proponen que la abundancia de las especies

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en los ambientes tropicales se debe a la antigüedad de estos, lo cual se correspondería con la antigüedad de muchos de sus linajes. Asimismo, Latham & Ricklefs (1993), Farrell & Mitter (1993), Hawkins et al. (2006) postulan que las dispersiones fuera de los trópicos hacia las regiones templadas serían más recientes y limitadas a algunos grupos. Por el contrario, otros investigadores proponen diferencias sustanciales entre las tasas de diversificación, siendo más altas en los ecosistemas tropicales respecto a los templados. De acuerdo con diversas propuestas, estas diferencias serían promovidas principalmente por factores como: 1) la deriva genética y procesos selectivos de pequeñas poblaciones que aceleran las tasas de especiación (Fedorov 1966; Schneider et al. 1999); 2) las variaciones climáticas que promueven la especiación en bajas latitudes (Haffer 1969; Vrba 1985,1995; Dynesius & Jansson 2000); 3) la alta probabilidad para la especiación simpátrica (Gentry 1989) y parapátrica (Moritz et al. 2000); 4) el mayor área de los ambientes tropicales provee más oportunidades para el aislamiento geográfico (Wright 1983; Rosenzweig 1995); 5) un rango fisiológico de tolerancia estrecho reduciría la dispersión hacia ambientes desfavorables (Janzen 1967; Ghalambor et al. 2006); 6) las altas temperaturas promueven el incremento de la velocidad en el cambio evolutivo (Allen et al. 2006); 7) las fuertes interacciones bióticas llevan hacia una mayor especialización y un incremento de la especiación (Dobzhansky 1950; Paine 1966; Schemske 2002); 8) la estabilidad climática de los ambientes tropicales reduce las tasas de extinción (Darwin 1859; Wallace 1878; Fischer 1960); 9) las áreas tropicales grandes promueven poblaciones grandes, amplios rangos de distribución y de esta manera bajas tasas de extinción (Rosenzweig 1995). Finalmente, la inclusión de una perspectiva filogenética en las diversas hipótesis evolutivas sería fundamental en el desarrollo de lo que se ha denominado el principio de la conservación del nicho (Wiens 2004; Losos 2008) o, lo que es lo mismo, la retención filogenética de características ecológicas ancestrales (Wiens 2004; Wiens et al. 2010).

Considerando lo anterior, podríamos afirmar que los patrones macroevolutivos son un entramado complejo de factores abióticos y bióticos actuando juntos en el marco de la contingencia evolutiva de cada clado (Benton 2009). En este contexto, una de las interpretaciones más integradoras fue la realizada por Vrba (1980, 1987). Esta establece un rol primario de los agentes abióticos (procesos geológicos y cambios climáticos) como principales promotores de especiación y extinción, modulado por los distintos niveles de especialización a unas condiciones

ambientales específicas, determinadas por la estructura y recursos de un bioma particular. Con lo cual, aquellas especies que son “especialistas” en el bioma de distribución que habitan, son mas susceptibles a altas tasas de especiación por eventos de vicarianza a partir de cambios ambientales o geológicos drásticos que puedan suceder en sus zonas de distribución. Por el contrario las “generalistas” ocupando varios biomas y adaptadas a una variedad amplia de condiciones fisiográficas, tendrán menores tasas de especiación y extinción (Vrba 1980; Vrba 1987, 1992, 1999). De esta manera, según la hipótesis de Vrba, biomas tropicales como las selvas lluviosas, con un régimen climático extremo de lluvia y temperatura, pero con una estabilidad anual, presentarían altas tasas de diversificación de especies debido a los constantes y alternantes procesos de expansión y contracción promovidos por cambios climáticos a lo largo de su historia (Vrba 1993). De esta manera, diversos aspectos abordados en las hipótesis expuestas anteriormente como: el tiempo, siendo uno de los biomas más antiguos y con mayor área (Fine & Ree 2006); su alta productividad primaria (Hawkins et al. 2003b); el desarrollo de adaptaciones morfofisiológicas en relación a la temperatura que serían posteriores limitaciones en la adaptación a nuevos ambientes (Ghalambor et al. 2006; Araújo et al. 2013); la tendencia filogenética hacia la conservación de diversas características ecológicas (Wiens & Graham 2005); así como otros aspectos relacionados con interacciones bióticas (Graham et al. 2006) estarían inmersos en este contexto explicativo. Esta visión macroevolutiva vincularía al bioma y su dinámica espacio-temporal en una visión integradora de las diversas hipótesis evolutivas expuestas y nos permitiría construir un marco teórico holístico para la comprensión de los procesos y patrones macroevolutivos de los organismos. En nuestro caso de las aves.

3. El concepto de Bioma en ecología y evolución.

Factores abióticos como el clima, la topografía y el suelo tienen un efecto en los caracteres presentes en las plantas y los animales, y por ende en la estructura de los ecosistemas (Ricklefs 2008). Aunque por cuestiones filogenéticas, espaciales e históricas dos localidades no compartan las mismas especies, se pueden clasificar las comunidades y los ecosistemas en categorías basadas en las condiciones climáticas y vegetales dominantes. Estas categorías reciben el nombre de biomas (Walter 1970; Whittaker 1975). Los ecosistemas pertenecientes a un mismo bioma compartirán una

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vegetación similar, así como un funcionamiento energético similar. Lo anterior hace que los biomas sean puntos de referencia para el estudio de muchos procesos a escala global (Hernández Fernández 2001; Hernández Fernández & Vrba 2005a; Moreno Bofarull et al. 2008; Ricklefs 2008; Cantalapiedra et al. 2011; Jetz & Fine 2012; Gómez Cano et al. 2013).

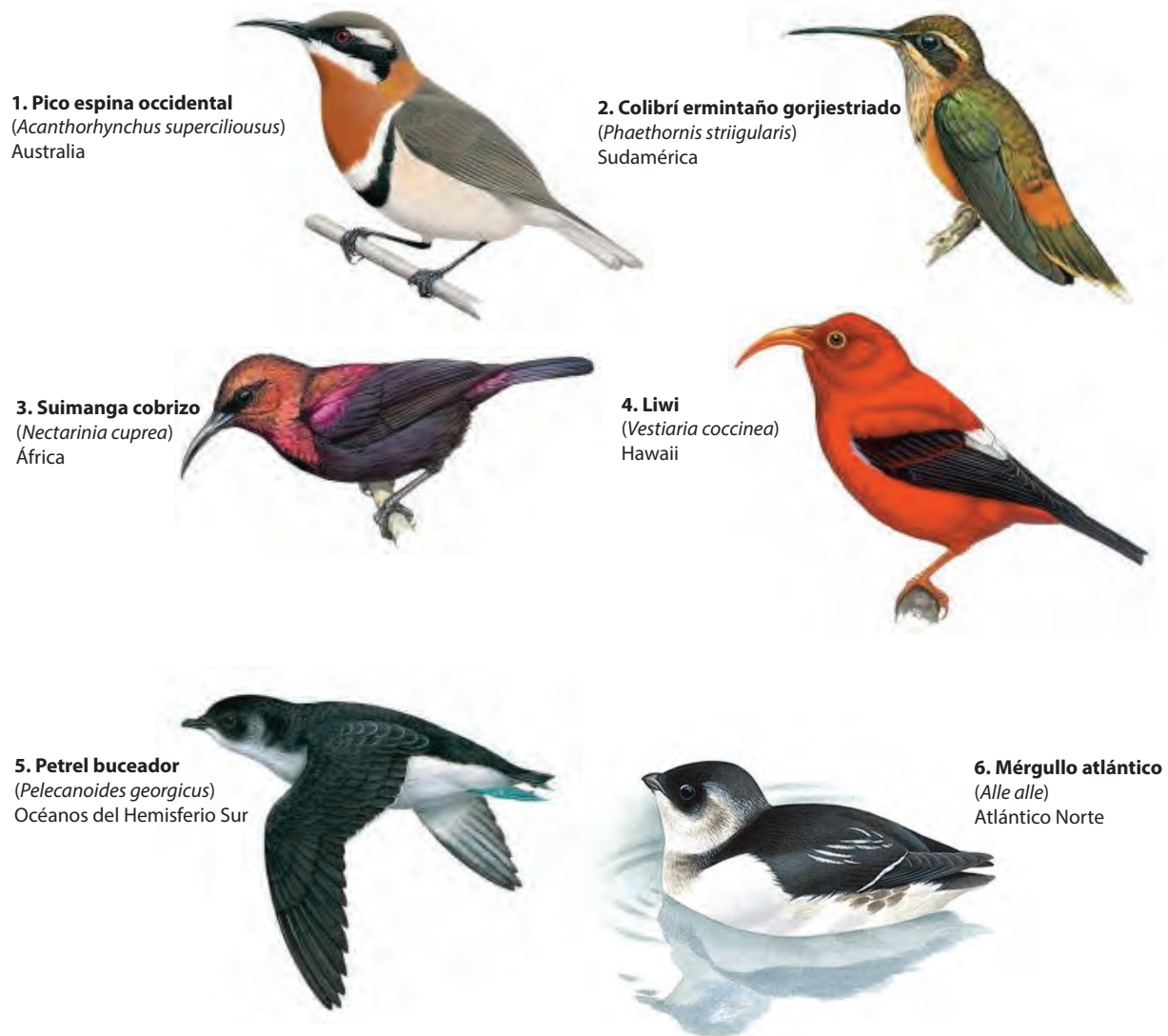


Figura 3. Convergencia morfológica en linajes de aves no emparentados ocupando hábitats y ambientes similares (arriba) aves nectarívoras de los bosques tropicales; (abajo) aves adaptadas a ambientes marinos.

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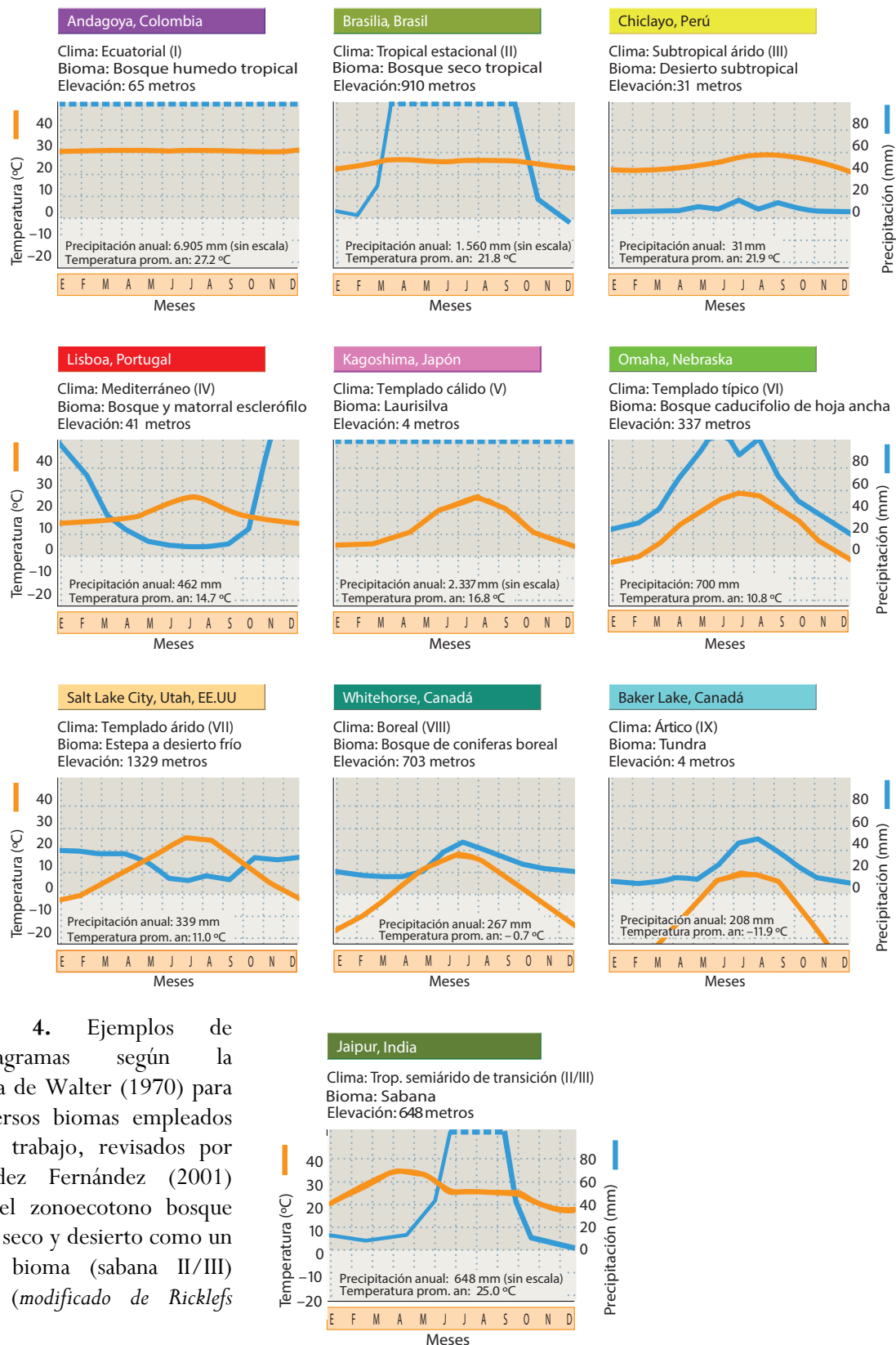


Figura 4. Ejemplos de climodiagramas según la tipología de Walter (1970) para los diversos biomas empleados en este trabajo, revisados por Hernández Fernández (2001) añadió el zonoecotono bosque tropical seco y desierto como un décimo bioma (sabana II/III) (abajo) (modificado de Ricklefs 2008).

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El bioma como escala de trabajo en macroecología y macroevolución cobra importancia debido a que integra una identidad histórica en términos de procesos tectónicos y climáticos que los han configurado (Pennington et al. 2004; Ricklefs 2008; Jetz & Fine 2012). Pese a su distancia geográfica, los ecosistemas de bosques lluviosos tropicales son similares en la Amazonía de Sudamérica, las selvas del Congo en África ecuatorial o las junglas de Indonesia (Plana 2004; Wong 2011; Jaramillo & Cárdenas 2013). A parte del régimen climático como principal determinante la vegetación en estos biomas, también existen importantes similitudes en su productividad, reciclaje de nutrientes y estructura de las comunidades animales, evidenciándose en estas últimas destacados procesos de convergencia (Ricklefs 2008)(Fig.3). Complementando a lo anterior, los biomas al establecerse como arenas evolutivas adquieren asimismo sus propias dinámicas evolutivas en términos de especiación y extinción en relación a sus procesos históricos (Woodward et al. 2004; Jetz & Fine 2012; Donoghue & Edwards 2014; Guerrero et al. 2014).

Diversos sistemas de clasificación han sido desarrollados para los biomas, sin embargo uno de los más aceptados y utilizados ha sido el desarrollado por Walter (1970). Este sistema originalmente en nueve divisiones, esta basado en los ciclos anuales de temperatura y precipitación (Fig.4). Los valores de temperatura y precipitación son usados para definir las zonas climáticas, las cuales se corresponden con las condiciones de humedad y estrés térmico fundamental para el desarrollo de las comunidades vegetales (Walter 1970). De esta manera, por ejemplo, el bioma de estepa esta definido por una zona climática continental (desiertos fríos) que implica un régimen de aridez con veranos cálidos o templados e inviernos fríos, condicionando una vegetación tipo pradera de gramíneas. La tipología de Walter (1970) es sencilla y tiene fácil correspondencia con otros sistemas desarrollados (Holdridge 1967; Whittaker 1975).

Asimismo, esta ha sido modificada y actualizada por Hernández Fernández (2001) con un décimo bioma (Sabana – II/III), originalmente ecotono entre el bosque seco tropical y el desierto, debido a la complejidad faunística e importancia que ha mostrado en estudios ecológicos y paleoecológicos (Hernández Fernández 2001; Jacobs 2004; Bird et al. 2005; Hernández Fernández et al. 2007; Bouchenak-Khelladi & Hodkinson 2011).

En tiempos recientes diversos autores han consolidado el bioma como importante escala de estudio en diversos trabajos que lo vinculan al análisis de la conservación de nicho (Crisp et al. 2009; Donoghue & Edwards 2014; Jara-Arancio et al. 2014), al estudio de procesos macroevolutivos en mamíferos y aves (Hernández Fernández & Vrba 2005a; Moreno Bofarull et al. 2008; Cantalapiedra et al. 2011; Gómez Cano et al. 2013; Pelegrin et al. 2015), así como a diversos trabajos que integran este concepto en estudios filogenéticos, macroecológicos y paleoclimáticos (Hernández Fernández et al. 2007; Jetz & Fine 2012; Guerrero et al. 2013; Cantalapiedra et al. 2014; Pelegrin et al. 2014a).

4. Objetivos

Esta investigación doctoral se encuentra enmarcada en un enfoque macroecológico y macroevolutivo, que mediante el análisis filogenético de la biogeografía y la paleobiogeografía, pretende generar una visión integradora para comprender los patrones de radiación, dispersión y adaptación de las aves no passeriformes. Para lo cual, esta tesis pretende analizar la relación histórica entre los cambios climáticos y geológicos globales ocurridos desde el Cretácico Superior y durante el Cenozoico en la configuración de estos patrones. De acuerdo con lo anteriormente expuesto, este proyecto de tesis doctoral se encuentra planteado bajo tres objetivos principales que se detallan a continuación:

1. Analizar la influencia de los cambios climáticos globales en los procesos de cladogénesis en las aves no passeriformes

A lo largo del tiempo, cambios y variaciones ambientales han logrado configurar zonas donde se propician los eventos de especiación, diversificación y extinción. Esto parece estar relacionado con las características ecológicas de los linajes afectados, y en particular con su grado de especialización ecológica. Por ello, tras realizar una exhaustiva caracterización ecológica de todas las especies actuales de aves no passeriformes, en el capítulo 2 de este trabajo se aborda la relación entre la especiación ecológica, los ambientes ocupados y la diversidad biológica en los diferentes grupos de aves no passeriformes. De esta manera empleando técnicas de análisis estadístico de amplia robustez hemos contrastado las hipótesis de E.S. Vrba acerca de la influencia de los cambios climáticos en los eventos de diversificación cladogenética. Asimismo,

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estos análisis nos permitieron analizar la influencia de la dieta o la capacidad de migrar a larga distancia en los patrones de especialización ecológica.

2. Analizar los patrones de dispersión paleobiogeográfica de las aves modernas (*Neornithes*)

Se ha realizado una amplia revisión del registro fósil de *Neornithes*, incluyendo la recopilación de información filogenética de diversos taxones extintos. Además, se ha logrado combinar esta información con datos procedentes de distribuciones de especies actuales, así como de las diferentes configuraciones climáticas y tectónicas de la tierra en los últimos 90 millones de años. Así, se pretende presentar una aproximación macroevolutiva mediante la reconstrucción filogenética de caracteres ancestrales que permita generar nuevas hipótesis sobre el origen geográfico y la diversificación de los diferentes linajes de aves modernas desde su aparición en el Cretácico Superior. Igualmente, se explora qué escenarios evolutivos resultarían viables para explicar los diferentes eventos de dispersión a lo largo del tiempo geológico. La integración de toda la información paleo- y neontológica permite abordar un estudio exhaustivo de la evolución geográfica de este grupo de vertebrados, proponiendo un nuevo escenario evolutivo a gran escala.

3. Analizar las vías de adaptación de dos diferentes linajes de aves a distintos regímenes climáticos

Exploramos cómo diferentes grupos de aves han logrado adaptarse a climas específicos así como a los nuevos climas que emergieron en diferentes periodos temporales. Para este fin se han elegido dos grupos de los que tenemos un conocimiento filogenético, ecológico y geográfico amplio: Galliformes y Falconiformes. Mediante la aplicación de nuevas técnicas de análisis comparativo basadas en programas de análisis estadístico en un marco filogenético, se determinan las posibles relaciones entre los diversos factores ecológicos y los procesos históricos que han permitido la ocupación de los diferentes biomas terrestres durante la evolución de los dos linajes de Aves. Asimismo, el análisis desde una perspectiva filogenética de los patrones obtenidos en los dos grupos de aves permiten evaluar la conservación de nicho, aplicada al contexto de especialización biómica en una escala temporal amplia. Esto permite el contraste con los cambios ambientales inferidos a partir de evidencias paleoambientales derivadas del registro geológico, datos

geoquímicos, paleobotánicos y de cambios faunísticos.

Acometer las tareas derivadas de estos objetivos nos permitirá profundizar en el conocimiento de procesos evolutivos observados a diferentes escalas, los cuales han dado forma a las faunas modernas. De esta manera, se podrán sugerir nuevas hipótesis evolutivas sobre las posibles condiciones ambientales responsables del origen, diversificación y extinción de los grupos taxonómicos estudiados.

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2 Biomic specialization





Ecological specialization and climate changes regulate global evolutionary patterns in non-passerine birds

2

*" The equatorial regions are, as far as the history of past and present life, [...]
an older world than the shown in temperate zones, where , by comparison, the
laws that have governed the progressive development of life have operated with
little control over countless time "*

Alfred Russel Wallace (1878)

*"... Most past ecosystems were constantly and repeatedly forced by climatic
changes to alter, dismantle, and reconstitute"*

Elisabeth S. Vrba (1993)

ABSTRACT

Although birds form the most diverse group of terrestrial vertebrates and their biology has been extensively documented, our understanding of their evolutionary history and its connection to current geographic distribution patterns is still incomplete. By combining extensive ecological new data with simulations, we demonstrate that patterns of biome occupation in birds are congruent with those previously reported for mammals. Overall, species restricted to a single biome are by far more abundant than expected by random evolutionary patterns. Non-migratory species showed a higher biome specialization than migratory species. Herbivorous species tend to be significantly more biome-restricted than faunivorous species, the omnivorous birds being found at an intermediate position. Biome specialists are particularly concentrated in extreme biomes as tropical rainforests, subtropical deserts, steppes and tundras.

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These findings highlight the universality of the resource-use hypothesis, which links climate forcing and different degrees of ecological specialization to the observed distribution of species across the globe.

Key words: Aves, Biome, Extinction, Macroecology, Macroevolution, Speciation.

2.2. INTRODUCTION

Evolution of species is undoubtedly linked to historical patterns of environmental change (Cracraft 1973; Barnosky 2001; Lister 2004; Weir and Schluter 2004; Douglas et al. 2006; Hawkins et al. 2006; Buckley and Jetz 2007; Roelants et al. 2007; Hawkins et al. 2012; Gómez Cano et al. 2013). The proposed main drivers of speciation and extinction are physical and environmental variations such as shifts in climate and tectonics acting at wide scales (Vrba 1992, 1995; Benton 2009; Finarelli and Badgley 2010), which inevitably have a major footprint in present species diversity and ecological gradients. Current patterns of biodiversity have been explored for decades and correlated with various factors such as niche conservatism (Ramos Pereira and Palmeirim 2013), clade age (Hawkins et al. 2006; Buckley et al. 2010; Kennedy et al. 2014), disparate diversification rates (Bromham and Cardillo 2003), as well as present climate (Francis and Currie 2003) among others (Vrba 1980; Willig et al. 2003; Voelker et al. 2010; Wiens et al. 2010; Fjeldså 2012; Jetz and Fine 2012; Araújo et al. 2013; Vrba 1987). But all the particularities and the heterogeneity observed in these approaches still need an integrative explanation [Hawkins 2006]. We here revisit deep-time evolutionary perspectives that merges species ecology and geographic diversification gradients with processes of past physical change to complement contemporary macroecological perceptions of the species distributions seen today across the globe.

In particular, we focus on the importance of the biome as a relevant macroecological and macroevolutionary unit (Vrba 1987; Hernández Fernández 2001; Jetz and Fine 2012) based on the idea that the degree of biome specialization of species has an important role on differential diversification among clades: the so-called resource-use hypothesis (Vrba 1987). Specialists in resources associated to one particular biome should experience higher speciation rates through vicariance events and directional selection due to fragmentation of biome distribution in relation with global environmental or geological changes. By contrast, biome generalists are more ecologically flexible and should not be substantially affected by fragmentation of their

geographical distributions and subsequent speciation in relation to global changes (Vrba 1987). However, although this resource-use hypothesis has been supported by previous studies based on both extinct and extant mammalian faunas (Vrba 1987; Hernández Fernández and Vrba 2005; Moreno Bofarull et al. 2008; Cantalapiedra et al. 2011; Gómez Cano et al. 2013), its general relevance for the evolution and their impact on the species gradients of other terrestrial organisms remains untested.

In this context, birds are a group of great interest for the analysis and study of macroecological and macroevolutionary models (Cardillo 1999; Penny and Phillips 2004; Cardillo et al. 2005; Diniz-Filho et al. 2007; Hawkins et al. 2007; Sibly et al. 2012) and, particularly, to test the universality of the resource-use hypothesis. They are the most abundant group of terrestrial vertebrates with near 10,000 extant species, distributed in all ecosystems over the world, and many aspects of their very diverse biology and ecology are widely known (Del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, 2002). Additionally, the particular characteristics of this group—mostly flying organisms including a significant number of large distance migrant species—allow for the study of the influence of high dispersal abilities in the general incidence of the resource-use hypothesis.

Therefore, for the first time here, we tested several subsidiary predictions of the resource-use hypothesis in all world non-passerine bird species (3951): 1) given a clade, we should find more biome specialist species than expected by chance, due to their higher rates of speciation; 2) different clades are expected to show different degrees of specialization, due to the differential distribution of their resources, particularly in relation to dietary requirements; 3) we should expect higher proportion of stenobiomic species in biomes placed in the extremes of the global climatic gradient, which underwent a higher degree of fragmentation and contraction during climatic fluctuations (e.g., Milankovitch cycles), since populations in those biomes are subject to a high incidence of vicariance. We tested these predictions using the biomic specialization index (BSI), which is based in the number of inhabited biomes by each species (Hernández Fernández and Vrba 2005).

Drawing from an extensive review of ecological literature, we compiled a dataset including biome occupation, diet and migratory behavior for all non-passerine birds. Using Monte Carlo simulations, we tested whether the observed distribution of bird species across biomes is different from a scenario where biome specialization is independent from clades, biomes and diets. We found that the distribution of species restricted to a single biome is consistent with the predictions derived from the

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resource-use hypothesis and resembles those previously reported for mammals. There are more species restricted to a single biome (biome specialists) than expected under random simulations and these biome specialists are preferentially associated to extreme biomes. Although this pattern is maintained across different ecological types, there are differences associated to migratory status and diet. Non-migratory species showed a higher biome specialization than migratory species. Additionally, herbivorous species tend to be significantly more biome-restricted than faunivorous species, the omnivorous birds being found at an intermediate position.

2.3. MATERIALS AND METHODS

2.3.1. Data and study scale

This research was conducted at the global scale, considering all non-passerine birds (3951 species), which are included in 99 families. The basis of our study is the geographic distribution of each species. Distribution areas due to introduction by humans were excluded and species that became extinct in the last two centuries were included. For phylogenetic consistency, we followed the families-level taxonomy of Howard & Moore (Howard and Moore 2013). Information about the geographic distributions, dietary and migratory habits of birds species was gathered from Del Hoyo and co-workers (Del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, 2002) and refined with additional information from IUCN Red List (IUCN 2012) and BirdLife International Database (International. 2013).

2.3.2. Bioclimatic characterization of the species

Based on the distribution of its breeding area across the world, we computed the biomic specialization index (BSI) (Hernández Fernández and Vrba 2005) for each bird species, which indicates the number of inhabited climate zones (biomes). Biome occupation was established following the biomes defined and classified by Walter (Walter 1970) (Table 1). The decision on the number of climate zones inhabited by a species was based on the following. If 15% or more of the geographical range of a species is situated within a climate zone, the species was recorded as present in that climate zone. Since some climatic dominions are small enough to comprise less than 15% of the total distribution ranges of species with large range sizes, a species was also recorded as present in a specific climate zone if it inhabits 50% or more of one climatic dominion (Hernández Fernández 2001). We also considered those species inhabiting mountainous ranges as adapted to the biomes represented by analogous climatic series

Table 1. Biome typology used and its correspondence with vegetation types in the world (Modified from Walter 1970 , we consider II/III as a independent zonobiome -see Chapter1-).

Biome	
I	Evergreen tropical rainforest
II	Tropical deciduous woodland
II/III	Savanna
III	Subtropical desert
IV	Sclerophyllous woodland and shrubland
V	Temperate evergreen forest
VI	Broad-leaf deciduous forest
VII	Steppe/cold desert
VIII	Boreal coniferous forest (Taiga)
IX	Tundra.

of altitudinal gradients, since these habitats present similar vegetation physiognomy, ecological pressures and fragmentation dynamics during the climatic changes and fluctuations (Cantalapiedra et al. 2011).

Biome specialists (stenobiomic species) were defined as species that inhabit only one biome, hence has a $BSI = 1$ (Hernández Fernández and Vrba 2005). On the contrary, generalists (eurybiomic species) were defined as those with $BSI > 1$, been potentially present in up to ten biomes. In turn, eurybiomic species can be subdivided in two categories: “semi-eurybiomic species” ($1 < BSI < 5$), and “extreme eurybiomic species” ($BSI \geq 5$) (Hernández Fernández and Vrba 2005).

2.3.3. Ecological chraracterization of the species traits

Since they are related to niche breath and dispersal capabilities, migratory status and diet are two factors that may affect the pattern of biome occupation. Thus, we constructed a database with dietary information and migratory status for all the species of non-passeriform birds as recorded in the literature. We codified for three dietary categories: faunivores ($n = 2021$), with a food source coming mainly from animal protein; herbivores ($n = 1473$), feeding mainly on plants (leaves, flowers, nectar, fruits or seeds); and omnivores ($n = 457$), which obtain their nourishment from both animal and plant material in a significant proportion. Many species present occasional

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or seasonal feeding on animal protein (Gill 2007), but these were here coded as herbivores when they mainly feed on plants during most of the year. Regarding the migratory status, we considered species as migratory when they present a well-distinguished breeding area ($n = 704$) and non-migratory when there are no differences between breeding and wintering areas ($n = 3247$). Finally, for the species with aquatic habits and water-related distribution, BSI was codified based on their breeding area.

2.3.4. *Analyses*

We tested the prediction that there should be an uneven distribution of biome specialists across clades and biomes and that some biomes should show higher incidence of these specialists than others using Monte Carlo simulations (MC). We compared the observed abundance of specialists and generalists with null models where the biome occurrence for each species was randomly distributed (Hernández Fernández and Vrba 2005). Since particular ecological features of each biome determine species richness (Jetz and Fine 2012), Importantly, in each biome specific ecological features have an effect on species richness in such a way that there is no reason to consider that all the biomes must have the same number of species in the null model. Due this, we conducted a randomization that places species in biomes randomly while constraining the observed species richness in each biome. The null models were obtained from 10,000 simulations. The significance (p -value) of the observed trends was assessed comparing the real against the simulated values (Hernández Fernández and Vrba 2005). Besides running the MC analyses for non-passerine birds as a whole ($n = 3951$), we also explored the potential influence of migration in the observed patterns analyzing the migratory ($n = 704$) and non-migratory ($n = 3247$) non-passerines independently.

The second prediction of the resource-hypothesis states that some clades should be more generalist than other groups because the resources they need to survive may be found in environments that differ vastly in climate. A special emphasis has been put in dietary differences (Vrba 1987; Hernández Fernández and Vrba 2005; Moreno Bofarull et al. 2008; Vrba 1980) and, therefore, we might expect differences in the patterns of specialization among birds with different diets. In particular, herbivorous lineages should harbor a higher proportion of specialist species than faunivorous lineages because herbivores are usually more restricted to feeding on plant species associated to specific climatic conditions. Therefore, we performed independent MC analyses for each family of non-passerine birds with more than 10 species (50 families, $n=3778$ species) as well as for species included in each of the three dietary groups. In

the family analyses we also performed independent MC analyses including and excluding migratory species.

Finally, the third prediction tested here suggests that biomes that underwent a higher degree of fragmentation and expansion due to climatic cycles should have a higher proportion of stenobiomic species than the rest of biomes. Particularly, the resource-use hypothesis predicts that biomes placed in the extremes of the global climatic gradient such as equatorial rainforest (I), desert (III), steppe (VII) and tundra (IX) should have more specialist species than transitional biomes. To evaluate this prediction, we employed the same MC simulations performed previously for all non-passerines and 50 non-passerine families independently. The null distributions of the frequency estimates for each analysis resulted from 10,000 random samples of proportions of biome specialist species in each biome. All the analysis were performed with R (R Development Core Team 2013).

2.3. RESULTS AND DISCUSSION

2.3.1. Specialization patterns

Our results show that the frequency distribution of specialization for the non-passerine birds is strongly right-skewed (Fig. 1A). The mean BSI is 2.3, with 38.7% of species inhabiting only one biome (BSI = 1), which is significantly higher than the expected proportion under random processes (Fig. 1A and Table 2). The proportions of semi-eurybiomic species (BSI = 2-4) are significantly lower than expected from random models (Fig. 1A and Table 2). These results agree with the first prediction of the resource-use hypothesis and are broadly consistent with the patterns obtained for mammalian faunas (Cantalapiedra et al. 2011; Hernández Fernández and Vrba 2005; Moreno Bofarull et al. 2008). By contrast, a mere 9.86% of the species inhabit five or more different biomes, and only one species (0.03%) showed the ecological versatility to occupy all the terrestrial biomes: the peregrine falcon (*Falco peregrinus*). This raptor species is an important predator adapted to a wide spectrum of environmental conditions with various subspecies inhabiting from the tundra to the rainforest (Del Hoyo et al. 1994, 1999; Gaston et al. 2004; Worgester and Ydenberg 2008). Despite their lower proportions, extreme-eurybiomic species ($BSI \geq 5$) mostly tend to be significantly overrepresented (Fig. 1A and Table 2). Overall, since the extinction rates are lower in extreme eurybiomic species than in semi-eurybiomic species, the former may have experimented a net increase in species over time although their rates of

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vicariance and speciation are very low, these results are also agree with the tendencies obtained for extinct and recent mammals (Hernández Fernández and Vrba 2005).

Migratory birds showed a pattern that resembles the general trend of the non-passerines, with a proportion of biome specialist species (32.5%) significantly above the null expectation. However, the migratory species revealed significantly higher values of BSI than non-migratory birds (Fig. 1B-D). We suggest that, although migratory species are constrained by their reproductive requirements in their breeding areas, the competition with resident birds in winter quarters and the relative distance between the breeding and the wintering zones (Bell 2000; Newton 2003; Thorup 2006), their physiological and behavioral adaptations possibly allow them to cope with a higher diversity of climate regimes than non-migratory ones (Klaassen 1996; Berthold et al. 2003; Thorup 2006; Salewski and Bruderer 2007).

2.3.2. Ecological specialization, families and diet habits

The second prediction of the resource-use hypothesis considers differences in the distribution of resources among the taxa due to their adaptations to diverse environments.

Table 2. Observed and simulated BSI values for non-passerine bird.

BSI	%	Monte Carlo Analysis			
		Mean %	Std.de v	Range	<i>p</i>
1	38.70	22.00	0.54	20.00 - 24.00	<0.001
2	27.90	33.00	0.74	30.00 - 36.00	<0.001
3	15.30	27.00	0.70	24.00 - 29.00	<0.001
4	8.25	13.00	0.48	11.00 - 15.00	<0.001
5	4.18	4.00	0.29	3.00 - 5.10	0.419
6	3.14	0.80	0.14	0.32 - 1.40	<0.001
7	1.11	0.10	0.05	0.00 - 0.40	<0.001
8	0.89	0.01	0.02	0.00 - 0.11	<0.001
9	0.51	0.00	0.00	0.00 - 0.05	<0.001
10	0.03	0.00	0.00	0.00 - 0.00	1.000

Frequencies of non-passerine bird species in each BSI and comparison with 10000 Monte Carlo simulations. %, Proportion of the total number of species (3951); *p*, probability of species in the simulations being greater than or equal to (plain) or lower than or equal to (italics) the observed proportion. Further information and details about results and data see also Supplementary file 1 for non-migratory and migratory birds and Supplementary file 2 for dietary groups.

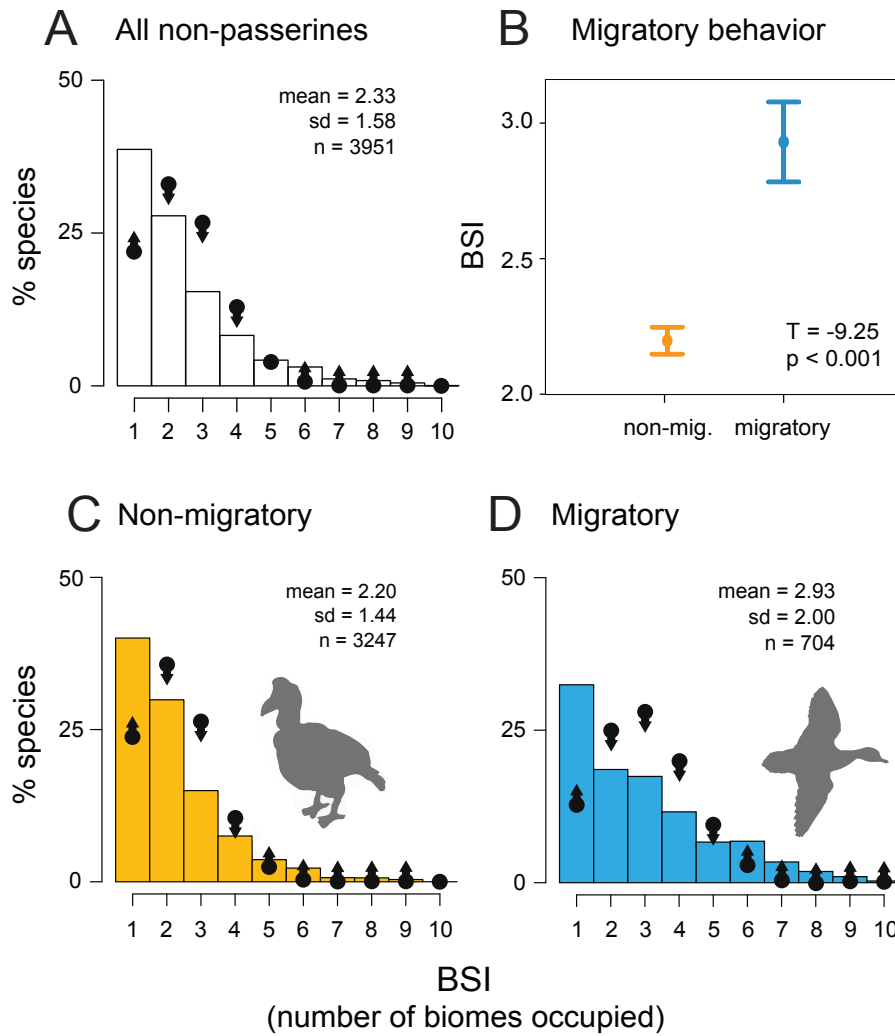


Figure 1. Biome specialization of non-passerine birds (A); bars represent the observed distribution of BSI and dots show the average percentage of species from 10,000 Monte Carlo simulations (Table 2); significant differences between observed and simulated values ($p < 0.05$) are shown with arrows. (B) Differences in biome specialization between migratory and non-migratory species. Detailed distributions of observed and simulated BSI are also shown for non-migratory (C) and migratory (D). More details in Table S1 and Supplementary Figures (Appendix 2.8).

Our results at the family level show substantial differences among families, indeed (Fig. 2, Fig.S1). Nevertheless, it is clear that there is still a much higher prevalence of specialist species than expected for the majority of the bird families (84%, Fig. 2) independently of their migratory status (Fig. 2, Appendix 2.8.3). Additionally, the patterns at the family level for generalist species were also similar to the general pattern, although they were less conspicuous (Fig. 2) probably associated to the lower species numbers of extreme generalists.

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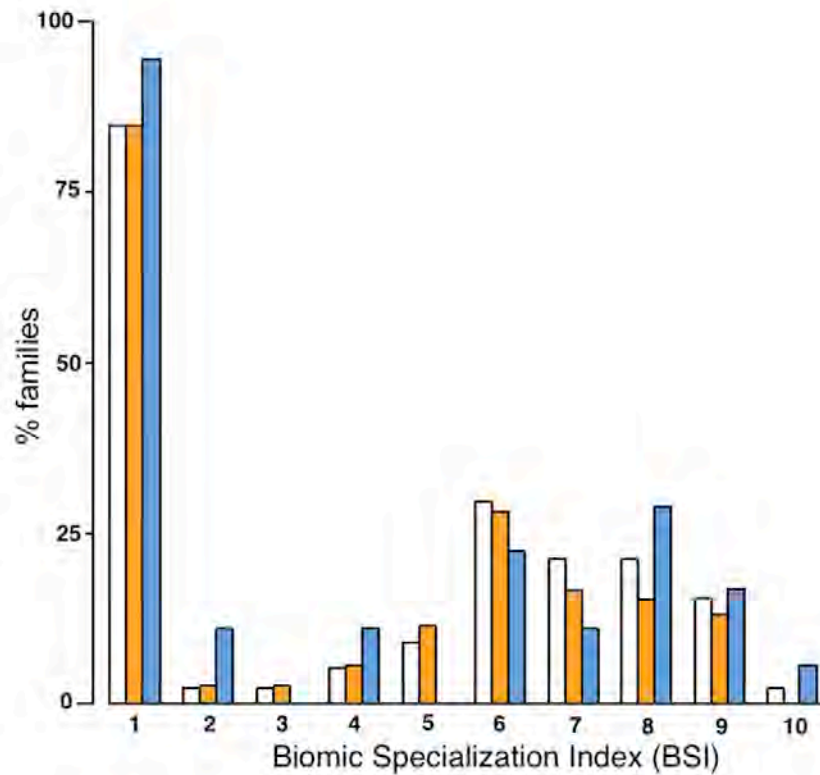


Figure 2. Biome specialization across non-passerine families. Frequencies of families with significantly higher proportion of species in a given BSI category than expected by chance. Only families with more than 10 species were analyzed (see Methods). Analyses were repeated for all the species (white, 50 families), excluding migratory species (orange, 44 families) and excluding non-migratory species (blue, 17 families). For additional information about results and data for each family see also supplementary Figures S1 to S4 (Appendix 2.8).

The three dietary groups showed striking similarities to the general pattern seen before, with prevalence of specialist species, underrepresentation of moderate generalists and overrepresentation of extreme generalist species (Fig. 3A-C). In any case, herbivores are significantly more biome-specialized than faunivores, which appear displaced towards higher BSI values, and omnivores are in an intermediate position (Fig. 3D).

Higher BSI values in faunivores (Fig. 3B) suggest that they can find their main food source in environments that differ vastly in climate, since they are not usually restricted to a particular prey species (Carbone et al. 1999; Carbone et al. 2007; Ingram et al. 2009; Sibly et al. 2012; Price et al. 2012). Additionally, many faunivorous bird lineages are adapted to aquatic environments (Fig. 2, Appendix 2.8), in these habitats they may find a great variety of resources such as fish or invertebrates

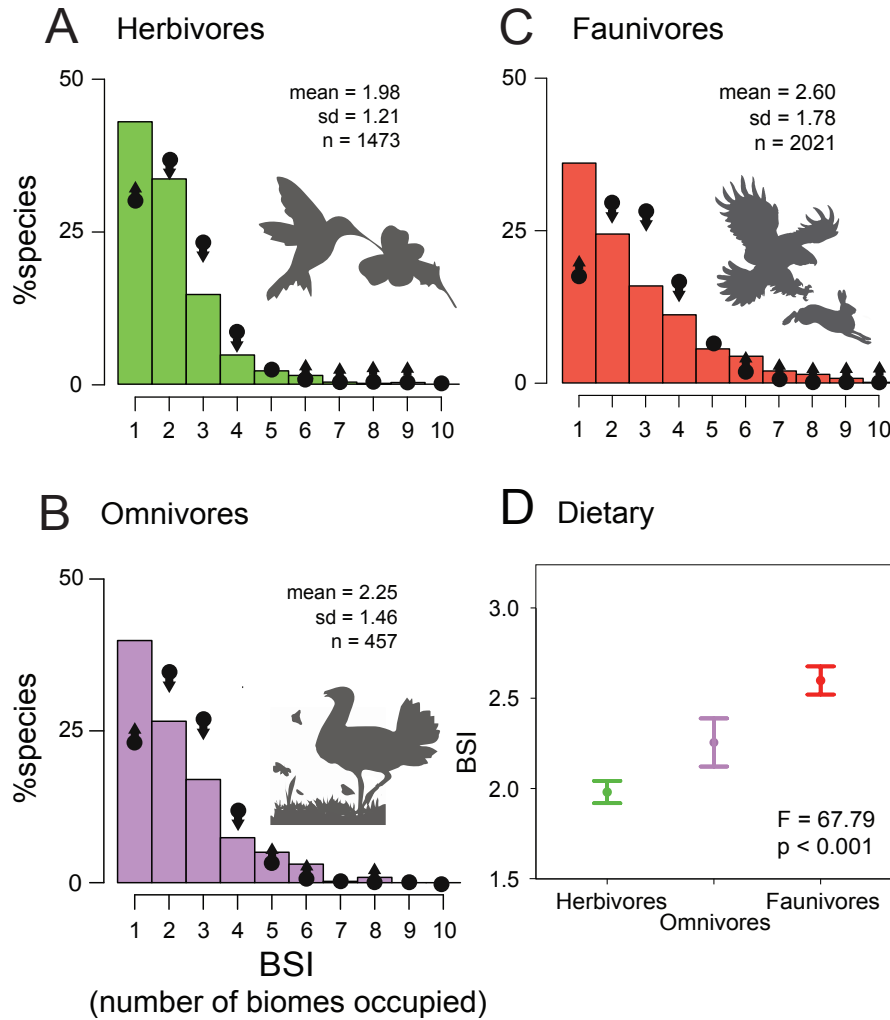


Figure 3. Biome specialization of non-passerine birds with different diets. Detailed distributions of observed and simulated BSI for herbivorous (A), faunivorous (B) and omnivorous (C) species. Bars represent the observed distribution of BSI; dots show the average percentage of species from 10,000 Monte Carlo simulations; and significant differences between observed and simulated values ($p < 0.05$) are shown with arrows. (D) Differences in biome specialization between three dietary groups. Further information and details about results and data see also Table S2 (Appendix 2).

(Cody 1973; Ballance et al. 1997; Van Tuinen et al. 2001; Steinmetz et al. 2003). Since these environments are often transversal to terrestrial biomes, these groups have been able to develop ecological and reproductive strategies in specialized niches, but with a lower dependency on terrestrial habitats and their resources, which allowed them to reach broad geographical distributions (Proches 2001; Buckton and Ormerod 2002; Steinmetz et al. 2003; Davies et al. 2010).

The clearer dominance of specialists among herbivorous species (Fig. 3A) could be related to morphological and physiological adaptations which allow them to exploit

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food resources from plants restricted to particular biomes (Gill 2007; Wheelwright 1985). Additionally, co-evolutionary relationships between reproductive strategies of plants and numerous herbivore birds (e.g. hummingbirds, parrots and toucans), which exert a positive selection for both parts (Wheelwright 1985; Flörchinger et al. 2010; Stiles 1981; Gill 2007), generate more opportunities for biome specialization in herbivore species. As an effect of the stability of this co-evolution process and the associated smaller geographic dispersions, the generation of diversity through niche subdivision may be facilitated (Price et al. 2012).

The intermediate position of omnivore (Fig. 3C) species can be considered as result of a compromise between the environmental restrictions associated to plant feeding and the versatility provided by facultative faunivory. Due to its ecological plasticity, omnivory appears as an important strategy to survive during seasons of limited food availability or times of environmental perturbation, which allows omnivorous species, inhabit different environments (Price et al. 2012; Vandermeer 2006).

2.3.3. *Avian specialization across different biomes*

During periods of climate shift, some biomes undergo contraction and fragmentation processes, which promote speciation and extinction. Because not all the biomes respond equally to such shifts, the resource-use hypothesis predicts differential evolutionary processes in different biomes, which in turn will render different proportions of biome specialists within them (Vrba 1992). Biomes located at the extremes of the global climatic gradient such as the equatorial rainforest (I), subtropical desert (III), steppe (VII) and tundra (IX) are more prone to fragmentation due to global climatic changes and, therefore, should be characterized by a clear overrepresentation of biome specialists.

Monte Carlo analysis revealed significantly high biome specialization in these biomes when all non-passerine birds were analyzed as a whole (Table 3, Fig. 4). The results for families (Fig. 2) were also coherent with the general pattern: most families showed overrepresentation of specialists in the rainforest, and substantial proportions of the families also presented more biome specialists than expected by chance in desert, steppe and tundra (Fig. 4). This distribution of specialization within clades is consistent with the third prediction. Interestingly, the rainforest showed the highest incidence (>60%) of families with statistically significant overrepresentation of specialists in a single biome. This is a biome with a much older origin and climatically more stable

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than the desert, steppe and tundra, which appeared during the last 5 million years (Potts and Behrensmeyer 1992).

Interestingly, two biomes that were not included in the prediction showed higher prevalence of specialist species than expected. This is the case for the tropical deciduous woodland (II) in both the complete analysis (Table 3) and in a substantial part of non-passerine families (Fig. 4 and Fig. 2). Such pattern has already been reported in previous works with mammals (Hernández Fernández and Vrba 2005; Cantalapiedra et al. 2011; Moreno Bofarull et al. 2008). Though this biome does not represent a climatic extreme, its historical dynamics in close association with the rainforest fluctuations and geological processes in African and American tropics (Williams et al. 1999; Hoorn et al. 2010). The heterogeneous mosaic structure of the deciduous woodlands (Williams and Pearson 1997; Hoorn et al. 2010; Jetz and Fine 2012) may have favored the survival of specialists in temporal refugia during climatic shifts (Haffer 1969; Mayr and O'hara 1986; Haffer 1997; Ribas et al. 2011). Also, the

Table 3. Observed and simulated distribution of stenobiomic non-passerine bird species (BSI = 1) across biomes.

Biome	Non-passerine birds			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	Std.d v	Range	<i>p</i>
I	1982	672	33.91	11.30	0.65	8.63 - 13.80	<0.001
II	1940	291	15.00	11.10	0.65	8.40 - 13.60	<0.001
II/III	926	49	5.21	7.38	0.83	4.75 - 10.70	<i>0.003</i>
III	401	45	11.22	6.28	1.20	2.24 - 11.20	<0.001
IV	515	21	4.08	6.51	1.10	3.11 - 11.10	<i>0.005</i>
V	1360	145	10.66	8.62	0.72	5.81 - 11.40	0.001
VI	640	35	5.47	6.73	0.97	3.59 - 10.90	<i>0.093</i>
VII	606	118	19.47	6.69	0.98	3.30 - 11.10	<0.001
VIII	569	40	7.08	6.56	1.00	3.01 - 10.40	0.371
IX	263	112	42.59	6.04	1.50	1.52 - 11.40	<0.001

sp., number of species; % proportion of species with BSI = 1 in relation to total number of species in each biome; *p*, probability in each biome of the proportion of species with BSI = 1 being greater than or equal to (plain) or lower than or equal to (*italics*) the observed proportion.

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subtropical evergreen forest (V) appears as an important environment for specialist species in around a quarter of the non-passerine families (Fig. 4). This biome extends through lowlands in humid subtropical areas, but it is also associated to montane environments in tropical regions (Still et al. 1999; Hewitt 2000). Therefore, historical climate dynamics along elevation gradients, which are responsible for multiple successive vicariance events, have created new opportunities for speciation stemming from isolated populations (Roy 1997; Bonaccorso and Guayasamin 2013; Quintero et al. 2013). Such processes have significantly contributed to the high richness and endemism in most tropical mountain areas (Fjeldsø and Lovett 1997; Kattan and Franco 2004; Kozak and Wiens 2007).

When the migratory status is taken into account, differences between migratory and non-migratory species are observed (Fig. 4 and Fig. 2, Appendix 2.8). While non-migratory species showed marked overspecialization in equatorial rainforest (I), migratory specialist species are much more abundant in tundra (IX) and subtropical desert (III) than expected by chance (Fig. 4). While the high productivity and habitat heterogeneity of the rainforest facilitates reproductive isolation and speciation in many sedentary clades (Ribas et al. 2011; Jetz and Fine 2012), thriving in the tundra and the desert requires a high degree of specialization in morphology, physiology and behavior.

Therefore, in such scenario, long distance migratory behavior could have worked as an adaptation of species to avoid seasonal shortage of food resources while preserving their reproductive niche (Sandercock et al. 2005; Jetz et al. 2008; García-Peña et al. 2009).

In the case of steppe (VII) and subtropical evergreen forest (V) inhabitants, the overrepresentation of specialists is found in substantially more families for non-migratory species than in migratory ones (Fig. 4). Sedentary species in these biomes are usually associated to tropical montane environments, which are particularly affected by climatic oscillations and have favored vicariance processes in many populations of tropical birds (Wiens and Rotenberry 1980; Fjeldsø 1992; Fjeldsø and Lovett 1997; Weir 2006; Bonaccorso and Guayasamin 2013) as commented before. Finally, there were higher percentages of families with more biome specialists than expected in migratory species of the taiga (VIII) and the savanna (II/III) than in the non-migratory ones (Fig. 4). This is probably related to the intense seasonality of these environments, following the resources rationale explained above for the tundra and the desert.

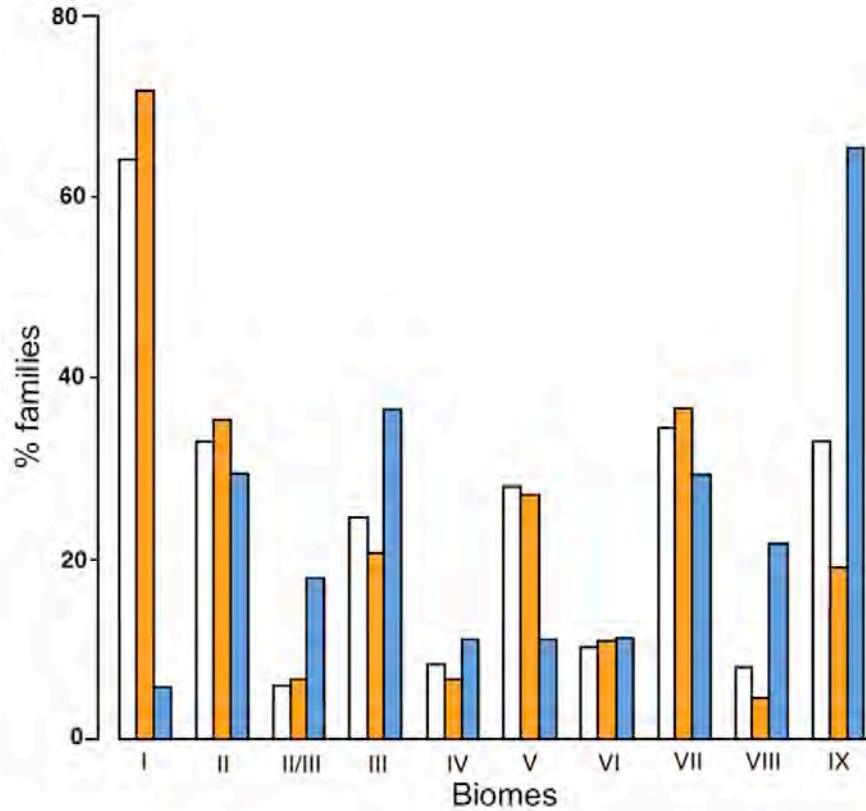


Figure 4. Biome specialization across non-passerine families and biomes. Frequencies of families presenting a significantly higher proportion of specialist species in a given biome when compared to simulations. Only families with more than 10 species were analyzed (see Methods). Analyses were repeated for all the species (white, 50 families), excluding migratory species (orange, 44 families) and excluding non-migratory species (blue, 17 families). Results and data for each family derived from Supplementary information of Fig.2 (Figures S1 to S4 in Appendix 2.8).

2.5. CONCLUSIONS

The resource-use hypothesis suggests that a key to understand patterns of diversity is to be found in historical processes: the turnover (speciation, extinction) of clades is related to abiotic changes. Our results present important evidences of the relationship between these processes and the evolution of non-passerine birds, in agreement with the predictions of the hypothesis. We found high frequency of species restricted to a single biome as a consequence of high speciation rates in biomes historically subjected to successive expansion-contraction-fragmentation processes during periods of climate change. This general pattern is maintained independently of the migratory behavior, although migratory species tend to be less specialized than non-migratory ones. Biome specialists are more abundant in herbivorous taxa than in omnivores or faunivores.

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Exceptions to the predictions of the resource-use hypothesis seem to be associated to montane biogeography and biome heterogeneity. Globally, the present contribution highlights the apparent universality of the resource-use hypothesis for terrestrial vertebrates, which for the first time has been tested using a non-mammalian clade.

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2.8. Appendix



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Appendix 2.8.1 - Table S1. Observed and simulated BSI values for non-migratory and migratory species.

BSI	Non Migratory %	Monte Carlo Analysis			
		Mean %	Std.dv.	Range	<i>p</i>
1	40.00	24.00	0.60	22.00 - 26.00	<0.001
2	30.00	36.00	0.85	33.00 - 39.00	<0.001
3	14.90	26.00	0.75	24.00 - 29.00	<0.001
4	7.51	11.00	0.49	8.90 - 12.00	<0.001
5	3.63	2.50	0.26	1.50 - 3.80	<0.001
6	2.28	0.36	0.11	0.07 - 0.82	<0.001
7	0.68	0.03	0.03	0.00 - 0.20	<0.001
8	0.65	0.00	0.01	0.00 - 0.07	<0.001
9	0.37	0.00	0.00	0.00 - 0.03	<0.001
10	0.00	0.00	0.00	0.00 - 0.00	1.000

BSI	Migratory %	Monte Carlo Analysis			
		Mean %	Std.dv.	Range	<i>p</i>
1	32.50	13.00	1.10	9.20 - 17.00	<0.001
2	18.30	25.00	1.50	20.00 - 30.00	<0.001
3	17.30	28.00	1.70	23.00 - 35.00	<0.001
4	11.60	20.00	1.40	16.00 - 25.00	<0.001
5	6.68	9.70	1.00	5.90 - 14.00	0.001
6	7.10	3.20	0.62	1.20 - 5.70	<0.001
7	3.12	0.69	0.31	0.00 - 2.10	<0.001
8	1.99	0.10	0.12	0.00 - 0.74	<0.001
9	1.14	0.01	0.03	0.00 - 0.30	<0.001
10	0.14	0.00	0.01	0.00 - 0.15	<0.001

Proportion of non-passerine bird species in each BSI category: non-migratory (n= 3247) and migratory (n = 704), and comparison with 10,000 Monte Carlo simulations. *p*, probability of species in the simulations being greater than or equal to (plain) or lower than or equal to (italics) the observed proportion.

Appendix 2.8.2. - Table S2. Observed and simulated BSI values for different dietary groups

BSI	Herbivores %	Monte Carlo Analysis			
		Mean %	Std.dv.	Range	<i>p</i>
1	42.60	30.00	0.96	25.00 - 33.00	<0.001
2	33.70	37.00	1.30	32.00 - 42.00	<i>0.004</i>
3	14.60	23.00	1.10	20.00 - 28.00	<0.001
4	4.68	8.30	0.66	6.10 - 11.00	<0.001
5	2.17	1.80	0.34	0.67 - 3.10	0.123
6	1.49	0.23	0.13	0.00 - 0.89	<0.001
7	0.34	0.02	0.04	0.00 - 0.23	<0.001
8	0.14	0.00	0.01	0.00 - 0.15	<0.001
9	0.27	0.00	0.00	0.00 - 0.07	<0.001
10	0.00	0.00	0.00	0.00 - 0.00	1.000
BSI	Omnivores %	Monte Carlo Analysis			
		Mean %	Std.dv.	Range	<i>P</i>
1	40.00	23.00	1.60	17.00 - 29.00	<0.001
2	26.50	35.00	2.30	26.00 - 43.00	<0.001
3	16.80	27.00	2.00	20.00 - 35.00	<0.001
4	7.44	12.00	1.40	6.60 - 17.00	<0.001
5	5.03	3.20	0.78	0.90 - 6.80	0.013
6	3.06	0.51	0.33	0.00 - 2.10	<0.001
7	0.22	0.05	0.11	0.00 - 0.71	0.243
8	0.88	0.00	0.03	0.00 - 0.46	<0.001
9	0.00	0.00	0.00	0.00 - 0.23	0.999
10	0.00	0.00	0.00	0.00 - 0.00	1.000
BSI	Faunivores %	Monte Carlo Analysis			
		Mean %	Std.dv.	Range	<i>P</i>
1	35.40	17.00	0.70	15.00 - 20.00	<0.001
2	24.00	30.00	0.96	26.00 - 33.00	<0.001
3	15.60	28.00	1.00	24.00 - 32.00	<0.001
4	11.00	17.00	0.77	14.00 - 20.00	<0.001
5	5.49	6.30	0.50	4.60 - 8.20	<i>0.050</i>
6	4.30	1.60	0.27	0.72 - 2.60	<0.001
7	1.93	0.26	0.12	0.00 - 0.78	<0.001
8	1.39	0.03	0.04	0.00 - 0.21	<0.001
9	0.74	0.00	0.01	0.00 - 0.10	<0.001
10	0.10	0.00	0.00	0.00 - 0.05	<0.001

Proportion of non-passerine bird species in each BSI category: Herbivores (n= 1473), Omnivores (n = 457) and Faunivores (n = 2021) and comparison with 10,000 Monte Carlo simulations. *p*, probability of species in the simulations being greater than or equal to (plain) or lower than or equal to (*italics*) the observed proportion.

2. Biomic specialization

Appendix 2.8.3. Supplementary data of Figure 2 (Fig. S1 from A to Q) – All species (Fam. >10 spp)

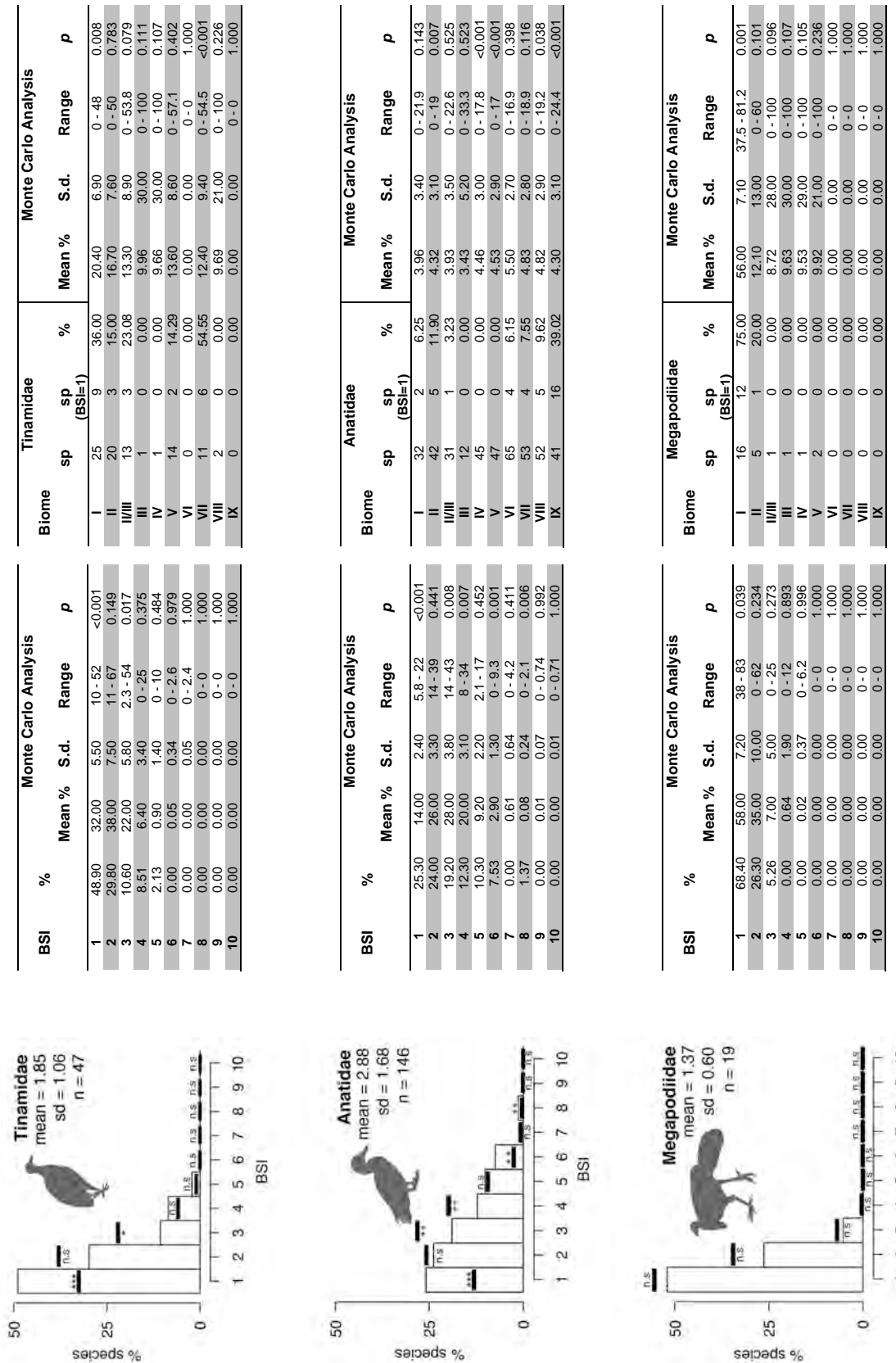


Figure 2-figure supplement 1A. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species in this plate: Tinamidae, Anatidae and Megapodiidae.

2. Biomic specialization

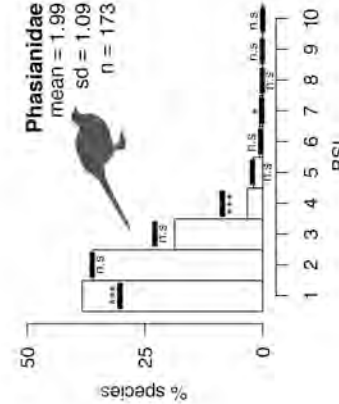
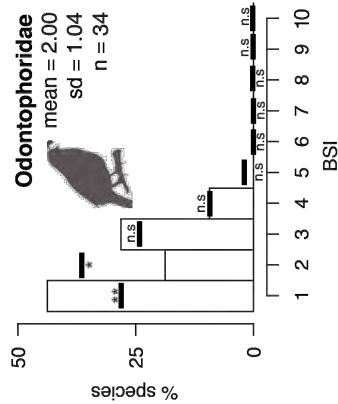
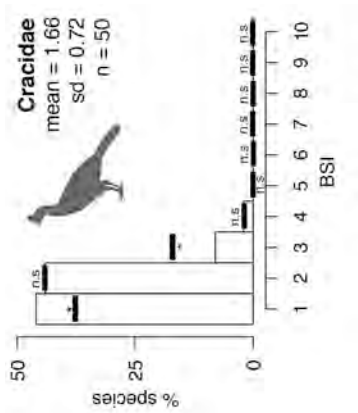


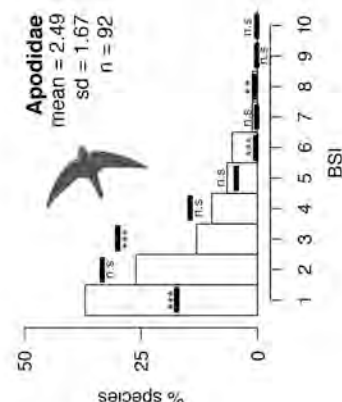
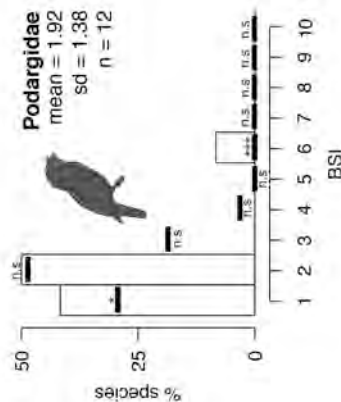
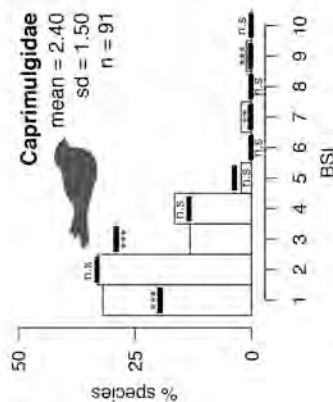
Figure 2-figure supplement 1B. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Cracidae, Odontophoridae and Phasianidae.

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	46.00	38.00	5.30	17 - 56	0.049	27.10	5.80	6.06 - 48.5	0.261
2	44.00	43.00	7.20	17 - 68	0.866	20.10	6.20	0 - 44.4	0.008
3	8.00	17.00	4.60	2.1 - 37	0.015	10.10	15.00	0 - 75	0.530
4	2.00	1.90	1.80	0 - 10	0.641	0.00	0.00	0 - 0	1.000
5	0.00	0.06	0.36	0 - 4.4	0.973	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000	9.87	17.00	0 - 100	0.366
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	44.10	29	6.30	7.1 - 53	0.005	14.30	8.60	0 - 53.8	<0.001
2	20.60	37	8.60	9.4 - 66	0.030	14.30	8.60	0 - 46.2	0.120
3	26.5	24	7.00	3.1 - 54	0.511	9.34	15.00	0 - 100	0.480
4	8.82	8.6	4.50	0 - 30	0.890	16.00	0 - 100	0.023	0.023
5	0.00	1.9	2.30	0 - 15	0.535	8.71	20.00	0 - 100	0.201
6	0.00	0.25	0.88	0 - 7.1	0.926	16.70	8.00	0 - 52.9	0.126
7	0.00	0.016	0.23	0 - 3.7	0.995	9.33	14.00	0 - 75	0.483
8	0.00	0.0013	0.064	0 - 3.2	1.000	8.99	16.00	0 - 100	0.329
9	0.00	0.00	0.00	0 - 0	1.000	10.40	11.00	0 - 71.4	<0.001
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	39.30	30.00	2.80	18 - 41	<0.001	12.60	4.60	0 - 31.9	<0.001
2	34.70	36.00	3.80	22 - 49	0.687	18.60	3.70	7.06 - 31.8	0.126
3	19.70	23.00	3.20	12 - 34	0.168	11.50	5.20	0 - 35.3	0.016
4	2.89	9.10	2.10	2.4 - 17	<0.001	9.65	9.70	0 - 55.6	0.007
5	1.73	2.20	1.10	0 - 7.8	0.444	10.20	7.90	0 - 42.9	<0.001
6	1.16	0.33	0.45	0 - 3.3	0.103	13.30	4.50	0 - 28	0.106
7	0.58	0.03	0.14	0 - 1.3	0.047	11.70	5.20	0 - 33.3	0.066
8	0.00	0.00	0.04	0 - 1.3	0.997	11.90	4.90	0 - 30.8	<0.001
9	0.00	0.00	0.00	0 - 0	1.000	10.80	6.20	0 - 45.8	0.327
10	0.00	0.00	0.00	0 - 0	1.000	9.16	21.00	0 - 100	0.010

2. Biomic specialization



BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	31.90	20.00	3.40	8.1 - 31	<0.001
2	33.00	33.00	4.80	16 - 51	0.898
3	13.20	29.00	4.60	13 - 45	<0.001
4	16.50	14.00	3.20	3.4 - 28	0.215
5	2.20	3.70	1.90	0 - 12	0.151
6	0.00	0.60	0.81	0 - 5.8	0.584
7	2.20	0.06	0.26	0 - 2.4	0.002
8	0.00	0.00	0.06	0 - 1.2	0.998
9	1.10	0.00	0.02	0 - 1.1	<0.001
10	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	41.70	29.00	8.70	0 - 60	0.020
2	50.00	49.00	14.00	8.3 - 92	0.712
3	0.00	18.00	9.20	0 - 45	0.057
4	0.00	3.20	4.60	0 - 18	0.652
5	0.00	0.31	1.60	0 - 9.1	0.964
6	8.33	0.01	0.32	0 - 9.1	<0.001
7	0.00	0.00	0.09	0 - 9.1	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	37.00	18.00	3.20	5.9 - 30	<0.001
2	26.10	33.00	4.70	17 - 52	0.078
3	13.00	30.00	4.80	13 - 48	<0.001
4	9.78	15.00	3.30	2.2 - 28	0.058
5	6.52	4.20	1.90	0 - 14	0.163
6	5.43	0.75	0.89	0 - 5.7	<0.001
7	1.09	0.08	0.29	0 - 2.3	0.071
8	1.09	0.01	0.08	0 - 1.2	0.005
9	0.00	0.00	0.01	0 - 1.1	1.000
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Caprimulgidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	46	10	21.74	8.61	3.80	0 - 26.1
II	56	11	19.64	11.1	3.80	0 - 26.8
III	34	4	11.76	6.83	4.20	0 - 29.4
IV	9	0	0.00	4.83	7.00	0 - 55.6
V	11	1	9.09	4.87	6.40	0 - 36.4
VI	33	1	3.03	6.73	4.20	0 - 24.2
VII	8	1	12.50	4.70	7.40	0 - 50
VIII	9	1	11.11	4.74	7.00	0 - 55.6
IX	12	0	0.00	4.93	6.20	0 - 41.7
X	0	0	0.00	0.00	0.00	0 - 0

Biome	Podargidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	11	5	45.45	27.00	8.50	0 - 45.5
II	7	0	0.00	5.40	6.90	0 - 14.3
III	1	0	0.00	2.50	16.00	0 - 100
IV	1	0	0.00	2.77	16.00	0 - 100
V	1	0	0.00	2.42	15.00	0 - 100
VI	1	0	0.00	2.25	15.00	0 - 100
VII	1	0	0.00	2.40	15.00	0 - 100
VIII	0	0	0.00	0.00	0.00	0 - 0
IX	0	0	0.00	0.00	0.00	0 - 0

Biome	Apodidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	60	19	31.67	9.72	3.40	0 - 23.3
II	55	6	10.91	8.41	3.40	0 - 25.5
III	16	1	6.25	4.00	4.80	0 - 31.2
IV	6	2	33.33	3.72	7.70	0 - 50
V	11	0	0.00	3.83	5.80	0 - 36.4
VI	39	5	12.82	5.80	3.60	0 - 25.6
VII	10	0	0.00	3.77	5.90	0 - 30
VIII	15	1	6.67	3.95	5.00	0 - 33.3
IX	13	0	0.00	3.96	5.30	0 - 30.8
X	4	0	0.00	3.42	9.10	0 - 75

Figure 2-figure supplement 1C. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Caprimulgidae, Podargidae and Apodidae.

2. Biomic specialization

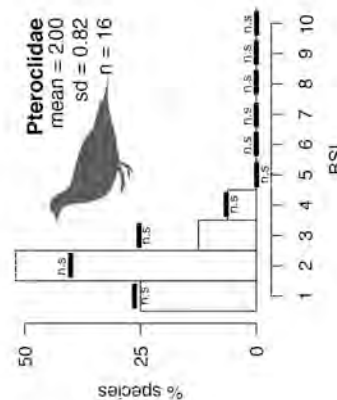
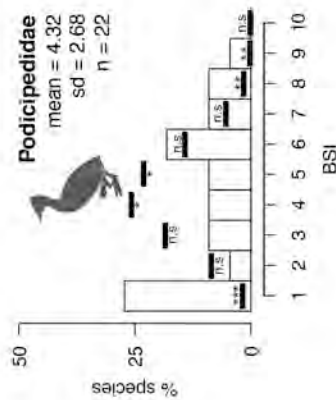
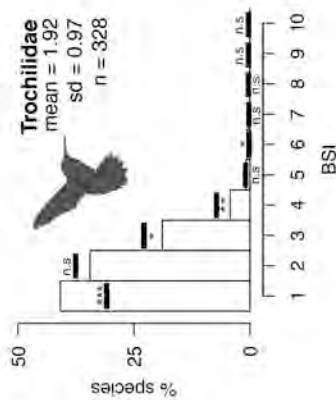


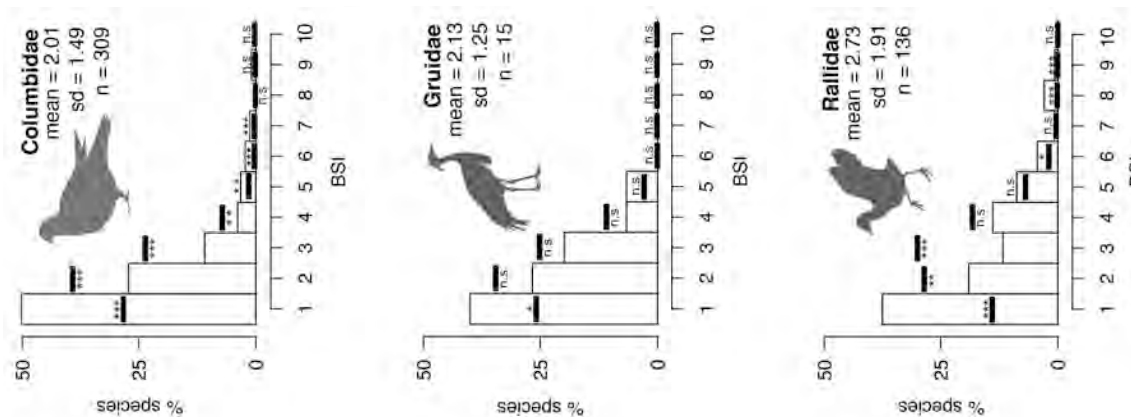
Figure 2-figure supplement 1D. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Trochilidae, Podicipedidae and Pteroclididae.

BSI						Monte Carlo Analysis						Trochilidae						Monte Carlo Analysis							
%		Mean %		S.d.		Range		p		Biome		sp		sp (BSI=1)		%		Mean %		S.d.		Range		p	
1	40.90	31.00	2.00	24 - 38	<0.001	I	158	41	25.95	17.50	2.70	8.23-27.8	0.001												
2	34.50	38.00	2.80	26 - 49	0.150	II	125	21	16.80	14.70	2.90	4 - 25.6	0.237												
3	18.90	23.00	2.20	15 - 31	0.036	III/III	34	3	8.82	10.10	5.00	0 - 32.4	0.836												
4	4.27	7.40	1.30	2.7 - 12	0.008	III	11	4	36.36	9.38	8.80	0 - 63.6	0.003												
5	0.92	1.30	0.62	0 - 4.8	0.346	IV	6	0	0.00	9.05	12.00	0 - 66.7	0.778												
6	0.61	0.11	0.19	0 - 1.4	0.045	V	150	33	22.00	16.70	2.70	7.33 - 28	0.022												
7	0.00	0.00	0.04	0 - 0.35	0.986	VI	8	0	0.00	9.40	10.00	0 - 62.5	<0.001												
8	0.00	0.00	0.01	0 - 0.34	1.000	VII	64	26	40.62	11.30	3.80	0 - 28.1	<0.001												
9	0.00	0.00	0.00	0 - 0	1.000	VIII	72	6	8.33	11.60	3.60	0 - 26.4	0.159												
10	0.00	0.00	0.00	0 - 0	1.000	IX	1	0	0.00	8.78	28.00	0 - 100	0.096												

BSI						Biome						Podicipedidae						Monte Carlo Analysis									
		%				Mean %		S.d.		Range		p		sp		sp (BSI=1)		%		Mean %		S.d.		Range		p	
1	27.30	2.20	3.00	0 - 18	<0.001	I	5	0	0.00	0.33	2.60	0 - 40	0.017	II	10	1	10.00	0.45	2.10	0 - 20	<0.001						
2	4.55	8.60	5.30	0 - 27	0.117	III/III	10	0	0.00	0.46	2.10	0 - 20	0.047	IV	7	0	0.00	0.36	2.30	0 - 28.6	0.025						
3	9.09	19.00	7.60	0 - 50	0.052	III	7	0	0.00	0.36	2.30	0 - 28.6	0.025	IV	11	0	0.00	0.53	2.20	0 - 18.2	0.061						
4	9.09	26.00	9.30	0 - 68	0.013	V	10	1	10.00	0.45	2.10	0 - 20	0.001	VI	14	0	0.00	0.71	2.20	0 - 14.3	0.108						
5	9.09	23.00	8.70	0 - 62	0.020	VII	14	3	21.43	0.68	2.20	0 - 14.3	<0.001	VIII	10	1	10.00	0.45	2.10	0 - 20	0.001						
6	18.20	14.00	6.70	0 - 41	0.225	IX	4	0	0.00	0.29	2.70	0 - 50	0.012														
7	9.09	5.70	4.50	0 - 27	0.139																						
8	9.09	1.40	2.40	0 - 19	0.004																						
9	4.55	0.20	0.95	0 - 9.1	0.004																						
10	0.00	0.01	0.23	0 - 4.5	0.997																						

Monte Carlo Analysis						Monte Carlo Analysis							
BSI	%	Monte Carlo Analysis				Biome		Pteroclidae		Monte Carlo Analysis			
		Mean %	S.d.	Range	p	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p	
1	25.00	27.00	8.90	0 - 56	0.498	I	0	0	0.00	0.00	0.00	0 - 0	1.000
2	56.20	40.00	13.00	0 - 93	0.107	II	9	0	0.00	14.40	10.00	0 - 55.6	<0.001
3	12.50	25.00	10.00	0 - 62	0.055	III/III	10	0	0.00	16.70	10.00	0 - 60	<0.001
4	6.25	6.90	5.80	0 - 31	0.403	III	6	2	33.33	9.99	11.00	0 - 66.7	0.007
5	0.00	0.67	2.10	0 - 15	0.904	IV	3	0	0.00	7.59	15.00	0 - 100	0.275
6	0.00	0.00	0.00	0 - 0	1.000	V	0	0	0.00	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000	VI	0	0	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	VII	4	2	50.00	8.27	13.00	0 - 75	0.001
9	0.00	0.00	0.00	0 - 0	1.000	VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00	0.00	0.00	0 - 0	1.000

2. Biomic specialization



Biome	Columbidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	211	103	48.82	20.00	2.20	11.8 - 28.4
II	158	35	22.15	13.00	2.30	5.06 - 24.1
III/III	49	2	4.08	7.56	3.70	0 - 26.5
IV	25	2	8.00	6.91	5.00	0 - 32
V	22	0	0.00	6.81	5.40	0 - 36.4
VI	90	8	8.89	8.97	2.80	0 - 23.3
VII	19	0	0.00	6.67	5.70	0 - 36.8
VIII	25	5	20.00	6.86	5.00	0 - 28
IX	18	0	0.00	6.65	5.90	0 - 38.9
X	3	0	0.00	6.36	14.00	0 - 100

Biome	Gruidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	0	0	0.00	0.00	0.00	0 - 0
II	6	0	0.00	12.80	13.00	0 - 66.7
III/III	4	0	0.00	10.70	15.00	0 - 75
IV	0	0	0.00	0.00	0.00	0 - 0
V	2	0	0.00	8.79	20.00	0 - 100
VI	3	0	0.00	9.77	17.00	0 - 100
VII	5	1	20.00	11.70	14.00	0 - 80
VIII	6	3	50.00	12.70	13.00	0 - 66.7
IX	4	1	25.00	10.70	15.00	0 - 100
X	2	1	50.00	9.23	20.00	0 - 100

Biome	Rallidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	82	24	29.27	6.97	2.60	0 - 17.1
II	79	12	15.19	6.59	2.60	0 - 19
III/III	38	0	0.00	3.84	3.00	0 - 18.4
IV	10	0	0.00	3.05	5.40	0 - 30
V	29	0	0.00	3.50	3.40	0 - 20.7
VI	54	6	11.11	4.63	2.70	0 - 16.7
VII	31	3	9.68	3.57	3.30	0 - 22.6
VIII	27	4	14.81	3.44	3.40	0 - 25.9
IX	19	1	5.26	3.18	4.00	0 - 26.3
X	2	1	50.00	2.92	12.00	0 - 100

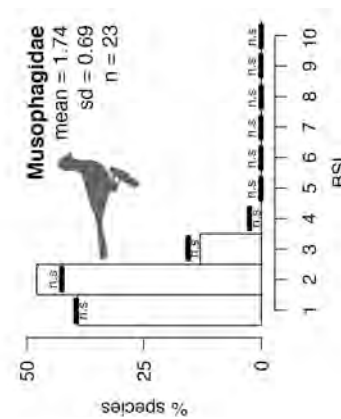
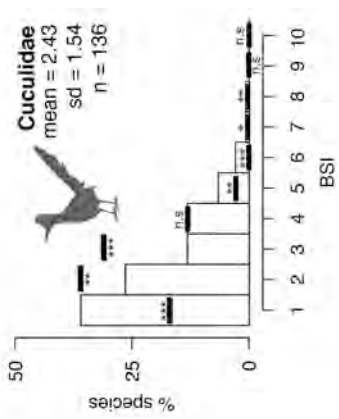
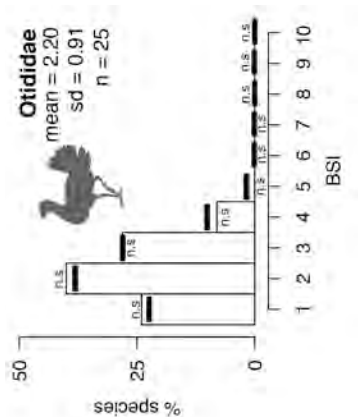
BSI	Monte Carlo Analysis			
	%	Mean %	S.d.	Range
1	50.20	28.00	2.00	20 - 35
2	27.20	39.00	2.80	29 - 50
3	11.00	24.00	2.20	15 - 34
4	3.88	7.30	1.30	2.7 - 12
5	3.24	1.30	0.62	0 - 3.8
6	2.27	0.13	0.21	0 - 1.4
7	1.29	0.01	0.05	0 - 0.36
8	0.00	0.00	0.01	0 - 0.35
9	0.97	0.00	0.00	0 - 0
10	0.00	0.00	0.00	0 - 0

BSI	Monte Carlo Analysis			
	%	Mean %	S.d.	Range
1	40.00	26.00	9.40	0 - 57
2	26.70	34.00	13.00	0 - 93
3	20.00	25.00	11.00	0 - 75
4	6.67	11.00	7.50	0 - 45
5	6.67	2.90	4.40	0 - 27
6	0.00	0.47	1.80	0 - 15
7	0.00	0.04	0.54	0 - 9.1
8	0.00	0.00	0.00	0 - 0
9	0.00	0.00	0.00	0 - 0
10	0.00	0.00	0.00	0 - 0

BSI	Monte Carlo Analysis			
	%	Mean %	S.d.	Range
1	37.50	14.00	2.50	5.2 - 24
2	19.10	29.00	3.60	14 - 43
3	11.80	30.00	4.00	16 - 44
4	14.00	18.00	3.00	7.5 - 31
5	8.82	6.80	2.00	0.75 - 17
6	4.41	1.60	1.00	0 - 6.9
7	0.74	0.22	0.40	0 - 2.3
8	2.94	0.02	0.11	0 - 1.6
9	0.74	0.00	0.02	0 - 0.77
10	0.00	0.00	0.00	0 - 0

Figure 2-figure supplement 1E. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Columbidae, Gruidae and Rallidae.

2. Biomic specialization



BSI	%	Monte Carlo Analysis				Monte Carlo Analysis							
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p				
1	24.00	22.00	6.60	0 - 48	0.624	I	0	0	0.00	0.00	0 - 0	1.000	
2	40.00	38.00	9.80	4.2 - 80	0.658	II	12	1	8.333	8.16	7.20	0 - 41.7	0.332
3	28.00	28.00	8.50	4 - 64	0.965	III/III	18	3	16.67	15.30	7.00	0 - 50	0.376
4	8.00	9.60	5.20	0 - 33	0.368	III	12	1	8.333	8.04	7.20	0 - 41.7	0.324
5	0.00	1.50	2.30	0 - 17	0.692	IV	7	1	14.29	5.82	8.60	0 - 57.1	0.055
6	0.00	0.10	0.64	0 - 9.1	0.977	V	2	0	0.00	4.63	15.00	0 - 100	0.099
7	0.00	0.00	0.10	0 - 4.8	1.000	VI	1	0	0.00	4.34	20.00	0 - 100	0.045
8	0.00	0.00	0.00	0 - 0	1.000	VII	3	0	0.00	4.79	12.00	0 - 66.7	0.159
9	0.00	0.00	0.00	0 - 0	1.000	VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00	0.00	0.00	0 - 0	1.000

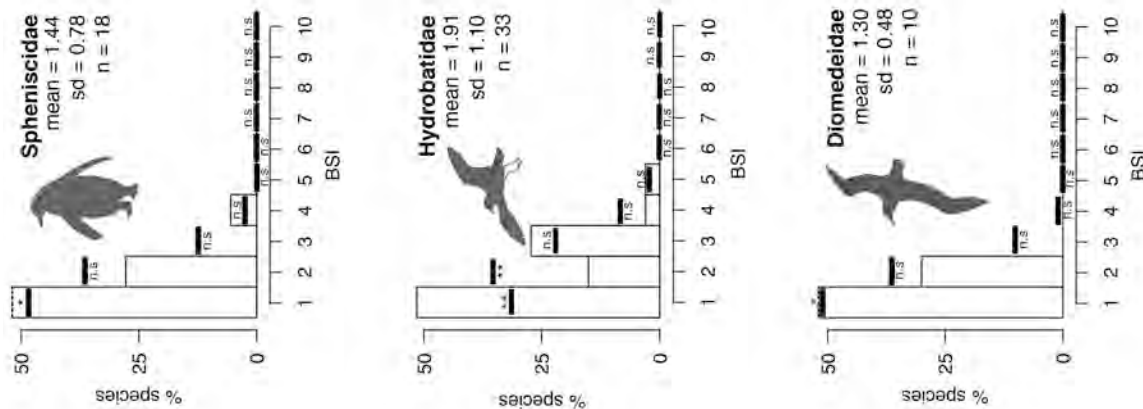
Biome	Otididae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	0	0	0.00	0.00	0.00	0 - 0	1.000
II	12	1	8.333	8.16	7.20	0 - 41.7	0.332
III/III	18	3	16.67	15.30	7.00	0 - 50	0.376
III	12	1	8.333	8.04	7.20	0 - 41.7	0.324
IV	7	1	14.29	5.82	8.60	0 - 57.1	0.055
V	2	0	0.00	4.63	15.00	0 - 100	0.099
VI	1	0	0.00	4.34	20.00	0 - 100	0.045
VII	3	0	0.00	4.79	12.00	0 - 66.7	0.159
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Biome		Cuculidae				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	sp	sp	sp	sp	Mean %	S.d.	Range	p		
1	36.00	17.00	2.50	8.5 - 26	<0.001	I	103	37	35.92	10.60	2.60	0.97-22.3	<0.001		
2	26.50	36.00	3.90	22 - 52	0.008	II	90	9	10.00	7.57	2.40	0 - 17.8	0.126		
3	13.20	31.00	3.80	17 - 48	<0.001	II/III	40	2	5.00	3.68	2.90	0 - 17.5	0.214		
4	13.20	13.00	2.40	3 - 22	0.805	III	5	0	0.00	2.68	7.20	0 - 40	0.147		
5	6.62	2.80	1.30	0 - 9.3	0.007	IV	11	0	0.00	2.76	5.00	0 - 36.4	0.356		
6	2.94	0.33	0.49	0 - 3.1	<0.001	V	45	1	2.22	3.86	2.80	0 - 15.6	0.188		
7	0.74	0.03	0.14	0 - 1.5	0.036	VI	18	0	0.00	2.93	3.90	0 - 22.2	0.728		
8	0.74	0.00	0.02	0 - 0.77	0.001	VII	9	0	0.00	2.71	5.40	0 - 33.3	0.282		
9	0.00	0.00	0.01	0 - 0.75	1.000	VIII	8	0	0.00	2.74	5.70	0 - 37.5	0.250		
10	0.00	0.00	0.00	0 - 0	1.000	IX	2	0	0.00	2.42	11.00	0 - 100	0.050		

BSI	%	Monte Carlo Analysis				Musophagidae				Biome				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	sp	sp (BSI=1)	%	sp	sp	Mean %	S.d.	Range	p			
1	39.10	40.00	6.40	18 - 61	0.990				6	1	16.67	4.59	8.10	0 - 33.3	0.018		
2	47.80	43.00	10.00	8.7 - 82	0.323				21	7	33.33	38.00	6.50	14.3 - 61.9	0.150		
3	13.00	16.00	5.90	0 - 38	0.270				III/II	6	1	16.67	4.56	8.00	0 - 33.3	0.017	
4	0.00	2.00	2.70	0 - 18	0.622				III	0	0	0.00	0.00	0.00	0 - 0	1.000	
5	0.00	0.00	0.00	0 - 0	1.000				IV	0	0	0.00	0.00	0.00	0 - 0	1.000	
6	0.00	0.00	0.00	0 - 0	1.000				V	7	0	0.00	4.72	7.40	0 - 28.6	0.442	
7	0.00	0.00	0.00	0 - 0	1.000				VI	0	0	0.00	0.00	0.00	0 - 0	1.000	
8	0.00	0.00	0.00	0 - 0	1.000				VII	0	0	0.00	0.00	0.00	0 - 0	1.000	
9	0.00	0.00	0.00	0 - 0	1.000				VIII	0	0	0.00	0.00	0.00	0 - 0	1.000	
10	0.00	0.00	0.00	0 - 0	1.000				IX	0	0	0.00	0.00	0.00	0 - 0	1.000	

Figure 2-figure supplement 1F: Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Otididae; Cuculidae and Musophagidae.

2. Biomic specialization



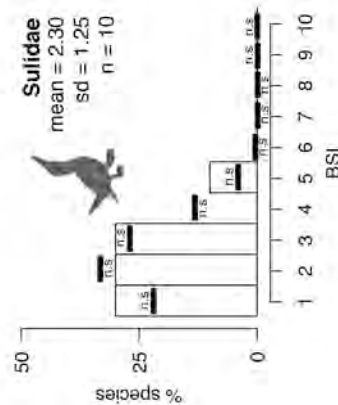
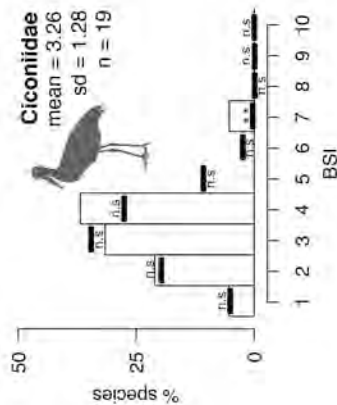
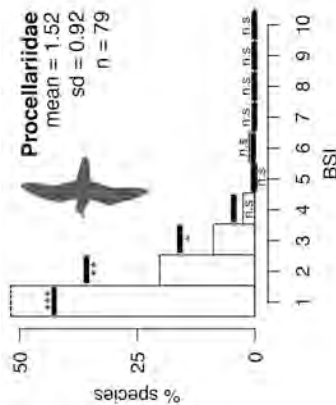
Monte Carlo Analysis					Monte Carlo Analysis							
BSI	%				Spheniscidae			Biome				
		Mean %	S.d.	Range	p	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	66.70	48.00	9.40	8.3 - 76	0.012	0	0	0.00	0.00	0.00	0 - 0	1.000
2	27.80	36.00	12.00	0 - 86	0.328	1	1	100.00	14.90	36.00	0 - 100	<0.001
3	0.00	13.00	7.30	0 - 46	0.083	0	0	0.00	0.00	0.00	0 - 0	1.000
4	5.56	2.30	3.60	0 - 23	0.455	2	0	0.00	16.10	26.00	0 - 100	0.427
5	0.00	0.24	1.30	0 - 15	0.965	2	0	0.00	16.20	26.00	0 - 100	0.433
6	0.00	0.01	0.27	0 - 7.7	0.998	3	1	33.33	17.30	21.00	0 - 100	0.075
7	0.00	0.00	0.07	0 - 6.7	1.000	3	0	0.00	17.10	21.00	0 - 100	0.796
8	0.00	0.00	0.00	0 - 0	1.000	3	1	33.33	17.30	21.00	0 - 100	0.075
9	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000	12	9	75.00	43.20	11.00	8.33 - 83.3	<0.001

BSI					Monte Carlo Analysis					Hydrobatidae					Monte Carlo Analysis						
		%			Mean %	S.d.	Range		p			sp	sp (BSI=1)	%			Mean %	S.d.	Range		p
1	51.50	32.00	6.80	4 - 56					0.002	I	4	1	25.00		12.40	16.00		0 - 100		0.084	
2	15.20	35.00	8.70	6.5 - 67					0.009	II	4	0	0.00		12.40	16.00		0 - 100		0.709	
3	27.30	22.00	7.00	0 - 56					0.303	III/III	2	0	0.00		11.60	22.00		0 - 100		0.283	
4	3.03	8.40	4.60	0 - 27					0.057	III	7	3	42.86		14.10	13.00		0 - 71.4		0.006	
5	3.03	2.10	2.50	0 - 17					0.902	IV	7	0	0.00		13.90	13.00		0 - 71.4		<0.001	
6	0.00	0.34	1.10	0 - 8					0.904	V	9	2	22.22		15.00	11.00		0 - 66.7		0.147	
7	0.00	0.04	0.35	0 - 4.2					0.990	VI	11	2	18.18		16.30	11.00		0 - 63.6		0.346	
8	0.00	0.00	0.07	0 - 3.6					1.000	VII	3	1	33.33		12.00	19.00		0 - 100		0.038	
9	0.00	0.00	0.00	0 - 0					1.000	VIII	3	0	0.00		12.00	19.00		0 - 100		0.471	
10	0.00	0.00	0.00	0 - 0					1.000	IX	13	8	61.54		18.00	9.70		0 - 61.5		<0.001	

BSI					%					Monte Carlo Analysis				

Figure 2-figure supplement 1G. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Spheniscidae, Hydrobatidae and Diomedidae.

2. Biomic specialization



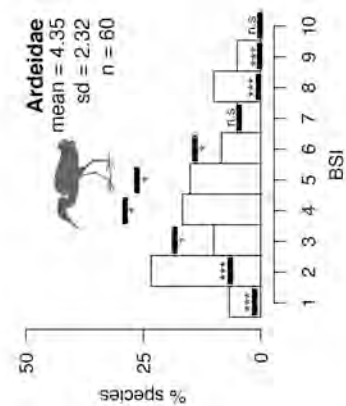
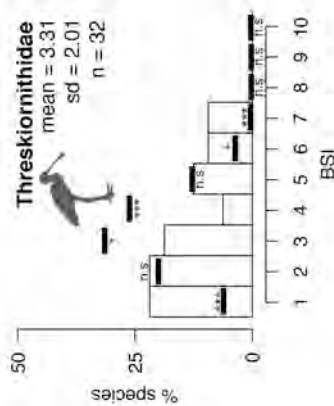
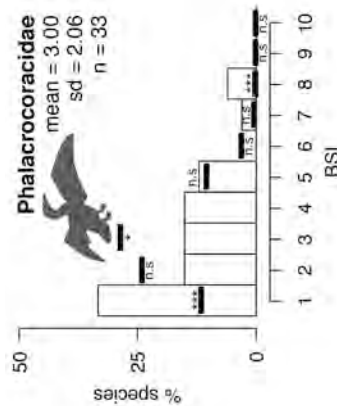
BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	67.10	43.00	4.80	22 - 60	<0.001	22.10	9.50	0 - 58.8	<0.001
2	20.30	36.00	5.90	14 - 58	0.004	18.70	17.00	0 - 100	0.004
3	8.86	16.00	4.10	3.2 - 34	0.034	18.20	22.00	0 - 100	0.006
4	2.53	4.30	2.30	0 - 15	0.239	18.40	22.00	0 - 100	0.007
5	0.00	0.72	1.00	0 - 7.8	0.618	20.00	12.00	0 - 80	0.138
6	1.27	0.07	0.34	0 - 3.5	0.048	28.10	7.30	33.3 - 56.7	0.013
7	0.00	0.01	0.09	0 - 1.7	0.996	21.90	9.80	0 - 62.5	0.101
8	0.00	0.00	0.02	0 - 1.6	1.000	20.10	12.00	0 - 70	0.134
9	0.00	0.00	0.00	0 - 0	1.000	18.40	22.00	0 - 100	0.843
10	0.00	0.00	0.00	0 - 0	1.000	24.70	8.20	0 - 65.2	<0.001

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	5.26	4.80	4.40	0 - 26	0.336	1.35	3.10	0 - 15.4	0.007
2	21.10	20.00	7.70	0 - 47	0.466	2.64	3.80	0 - 25	0.579
3	31.60	34.00	11.00	0 - 79	0.465	1.57	3.20	0 - 21.4	0.263
4	36.80	27.00	9.50	0 - 63	0.123	0.51	4.10	0 - 33.3	0.016
5	0.00	11.00	6.10	0 - 37	0.077	0.37	4.30	0 - 50	0.007
6	0.00	2.40	3.20	0 - 21	0.610	0.64	3.00	0 - 28.6	0.046
7	5.26	0.24	1.10	0 - 11	0.005	0.55	4.20	0 - 33.3	0.017
8	0.00	0.01	0.27	0 - 5.6	0.997	0.39	3.60	0 - 33.3	0.012
9	0.00	0.00	0.00	0 - 0	1.000	0.44	6.80	0 - 100	0.004
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	30.00	22.00	11.00	0 - 60	0.208	9.86	14.00	0 - 75	0.041
2	30.00	33.00	15.00	0 - 80	0.533	11.90	13.00	0 - 80	0.103
3	30.00	27.00	14.00	0 - 88	0.558	8.51	16.00	0 - 66.7	0.319
4	0.00	13.00	10.00	0 - 57	0.227	8.30	15.00	0 - 100	0.013
5	10.00	3.90	6.00	0 - 43	0.273	7.20	18.00	0 - 100	0.163
6	0.00	0.69	2.70	0 - 25	0.938	8.49	16.00	0 - 100	0.317
7	0.00	0.07	0.86	0 - 14	0.994	7.32	18.00	0 - 100	0.165
8	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000	6.55	25.00	0 - 100	0.070
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

Figure 2-figure supplement 1H. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Procellariidae, Ciconiidae and Sulidae.

2. Biomic specialization



Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	33.30	12.00	4.80	0 - 33	<0.001	I	5	0	0.00
2	15.20	24.00	6.70	3.1 - 52	0.071	II	11	1	9.09
3	15.20	28.00	7.90	0 - 61	0.031	III/IIII	7	0	0.00
4	15.20	21.00	6.80	0 - 52	0.168	III	11	1	9.09
5	12.10	10.00	4.80	0 - 30	0.576	IV	13	0	0.00
6	0.00	3.40	3.00	0 - 19	0.302	V	12	0	0.00
7	3.03	0.77	1.50	0 - 9.7	0.184	VI	16	3	18.75
8	6.06	0.11	0.58	0 - 6.7	<0.001	VII	11	3	27.27
9	0.00	0.01	0.16	0 - 3.3	0.997	VIII	4	0	0.00
10	0.00	0.00	0.03	0 - 3	1.000	IX	9	3	33.33

Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	21.90	6.30	3.80	0 - 22	<0.001	I	13	1	7.69
2	21.90	20.00	6.00	0 - 41	0.414	II	27	2	7.41
3	18.80	31.00	8.10	3.1 - 65	0.044	III/IIII	18	0	0.00
4	6.25	26.00	7.30	0 - 63	<0.001	III	8	0	0.00
5	12.50	13.00	5.20	0 - 33	0.779	IV	10	1	10.00
6	9.38	3.80	3.10	0 - 19	0.039	V	15	0	0.00
7	9.38	0.61	1.30	0 - 9.7	<0.001	VI	9	2	22.22
8	0.00	0.04	0.36	0 - 3.3	0.987	VII	5	1	20.00
9	0.00	0.00	0.06	0 - 3.2	1.000	VIII	1	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	6.67	1.10	1.30	0 - 8.3	<0.001	I	42	0	0.00
2	23.30	6.50	2.80	0 - 20	<0.001	II	55	2	3.64
3	10.00	18.00	4.40	3.3 - 35	0.013	III/IIII	34	0	0.00
4	16.70	29.00	5.70	10 - 52	0.009	III	20	0	0.00
5	15.00	26.00	5.40	6.7 - 50	0.011	IV	21	0	0.00
6	8.33	14.00	3.80	1.7 - 28	0.041	V	38	0	0.00
7	5.00	4.20	2.30	0 - 15	0.318	VI	30	2	6.67
8	10.00	0.65	0.99	0 - 6.7	<0.001	VII	14	0	0.00
9	5.00	0.04	0.24	0 - 3.4	<0.001	VIII	7	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

Figure 2-figure supplement 1I. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Phalacrocoracidae, Threskiornithidae and Ardeidae.

2. Biomic specialization

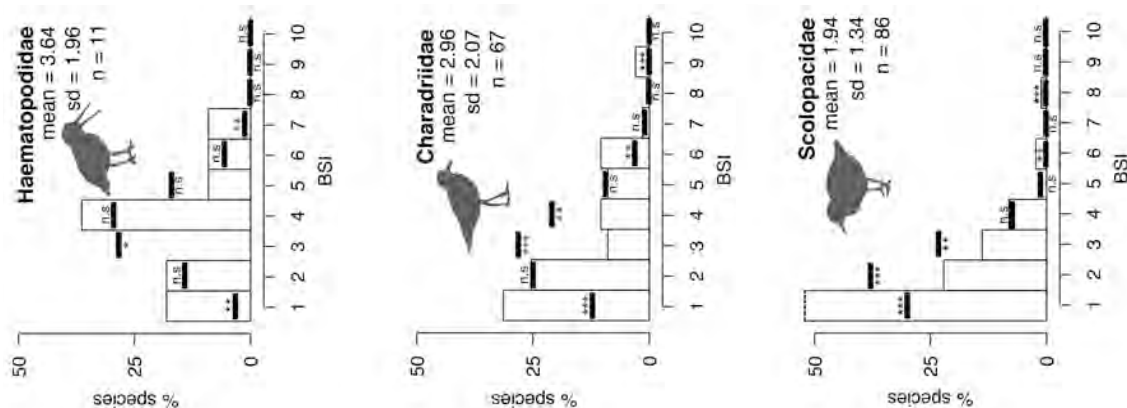


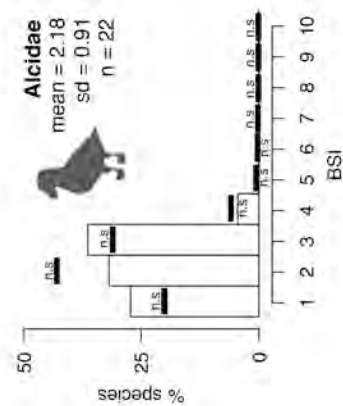
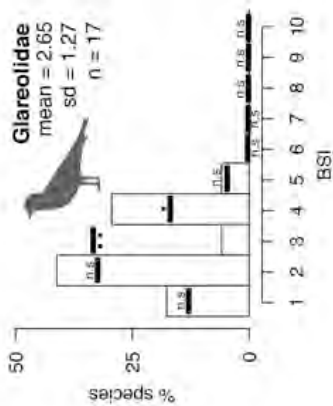
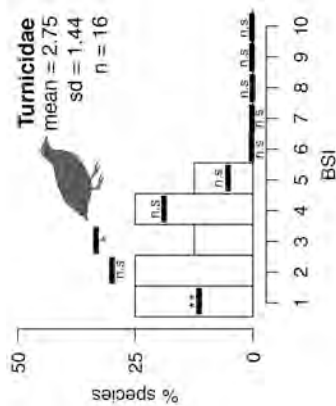
Figure 2-figure supplement 1J. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Haematopodidae, Charadriidae and Scolopacidae.

BSI	%	Monte Carlo Analysis				Haematopodidae			Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	Mean %	S.d.	Range	p
1	18.20	3.50	9.10	0 - 27	0.002	I	1	0	0.23	4.80	0 - 100	0.002
2	18.20	15.00	9.10	0 - 45	0.226	II	3	0	0.43	3.80	0 - 33.3	0.013
3	0.00	28.00	13.00	0 - 73	0.022	III/III	1	0	0.43	6.50	0 - 100	0.004
4	36.40	29.00	14.00	0 - 82	0.243	IV	4	0	0.53	3.60	0 - 50	0.022
5	9.09	17.00	10.00	0 - 55	0.107	V	8	1	1.20	3.70	0 - 25	0.002
6	9.09	5.80	6.30	0 - 30	0.145	VI	9	1	1.68	4.20	0 - 33.3	0.006
7	9.09	1.20	3.20	0 - 27	0.011	VII	7	0	0.89	3.50	0 - 28.6	0.066
8	0.00	0.11	1.00	0 - 10	0.988	VIII	4	0	0.50	3.50	0 - 25	0.021
9	0.00	0.01	0.26	0 - 10	0.999	IX	1	0	0.33	5.70	0 - 100	0.003
10	0.00	0.00	0.09	0 - 9.1	1.000		2	0	0.37	4.30	0 - 50	0.007

BSI						Monte Carlo Analysis							Charadriidae					Monte Carlo Analysis				
		%	Mean %	S.d.	Range	p	Biome		sp	sp (BSI=1)	%	Mean %	S.d.	Range	p							
1		31.30	12.00	3.40	1.5 - 27	<0.001	I	16	0	0.00	3.56	4.70	0 - 31.2	0.776								
2		25.40	25.00	4.80	9.1 - 44	0.789	II	34	5	14.71	5.42	3.70	0 - 20.6	0.006								
3		8.96	28.00	5.60	9.1 - 49	<0.001	III/III	22	0	0.00	3.97	4.10	0 - 22.7	<0.001								
4		10.40	21.00	4.70	4.5 - 39	0.008	III	17	0	0.00	3.59	4.40	0 - 35.3	0.882								
5		8.96	10.00	3.30	0 - 22	0.493	IV	24	0	0.00	4.19	4.00	0 - 25	<0.001								
6		10.40	3.30	2.00	0 - 12	0.002	V	21	1	4.76	3.89	4.10	0 - 28.6	0.238								
7		1.49	0.70	1.00	0 - 6.7	0.508	VI	24	3	12.50	4.11	3.90	0 - 25	0.013								
8		0.00	0.09	0.37	0 - 3.3	0.943	VII	22	9	40.91	3.99	4.00	0 - 27.3	<0.001								
9		2.99	0.01	0.11	0 - 1.6	<0.001	VIII	8	0	0.00	3.16	6.10	0 - 37.5	0.300								
10		0.00	0.00	0.03	0 - 1.6	1.000	IX	10	3	30.00	3.14	5.50	0 - 40	<0.001								

BSI		Monte Carlo Analysis				Scolopacidae				Monte Carlo Analysis			
	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	52.30	30.00	4.00	15 - 45	<0.001	I	5	1	20.00	8.64	12.00	0 - 80	0.066
2	22.10	38.00	5.40	20 - 57	<0.001	II	5	1	20.00	8.77	13.00	0 - 80	0.066
3	14.00	23.00	4.30	5.1 - 41	0.016	III/III	3	0	0.00	8.38	16.00	0 - 100	0.301
4	8.14	7.40	2.60	0 - 21	0.542	III	0	0	0.00	0.00	0.00	0 - 0	1.000
5	0.00	1.30	1.20	0 - 8.1	0.345	IV	4	0	0.00	9.04	14.00	0 - 75	0.458
6	2.33	0.12	0.39	0 - 3.8	0.004	V	12	3	25.00	9.59	8.30	0 - 50	0.020
7	0.00	0.01	0.08	0 - 1.4	0.996	VI	27	1	3.70	12.10	5.90	0 - 37	0.022
8	1.16	0.00	0.02	0 - 1.2	<0.001	VII	22	1	4.55	11.20	6.40	0 - 45.5	0.071
9	0.00	0.00	0.00	0 - 0	1.000	VIII	46	12	26.09	17.90	4.80	2.17-39.1	0.032
10	0.00	0.00	0.00	0 - 0	1.000	IX	43	26	60.47	16.70	5.00	2.33-37.2	<0.001

2. Biomic specialization



BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	25.00	12.00	6.60	0 - 38	0.010
2	25.00	30.00	10.00	0 - 69	0.283
3	12.50	33.00	12.00	0 - 80	0.014
4	25.00	19.00	8.40	0 - 50	0.199
5	12.50	5.30	5.00	0 - 29	0.066
6	0.00	0.70	2.10	0 - 13	0.893
7	0.00	0.03	0.44	0 - 6	0.995
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	17.60	13.00	6.50	0 - 35	0.174
2	41.20	32.00	10.00	0 - 65	0.153
3	5.88	33.00	11.00	0 - 81	0.001
4	29.40	17.00	7.70	0 - 47	0.049
5	5.88	4.30	4.40	0 - 25	0.330
6	0.00	0.51	1.70	0 - 13	0.917
7	0.00	0.01	0.29	0 - 1	0.998
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	27.30	20.00	6.30	0 - 41	0.093
2	31.80	43.00	10.00	9 - 82	0.133
3	36.40	31.00	8.30	0 - 68	0.283
4	4.55	6.10	4.30	0 - 25	0.240
5	0.00	0.44	1.40	0 - 10	0.908
6	0.00	0.01	0.22	0 - 5	0.998
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Turnicidae			Monte Carlo Analysis			
	sp	sp	(BSI=1)	Mean %	S.d.	Range	p
I	6	0	0.00	1.82	5.30	0 - 33.3	0.120
II	14	2	14.29	8.94	6.60	0 - 35.7	0.101
III/III	9	1	11.11	2.52	4.90	0 - 22.2	0.011
III	1	0	0.00	1.23	11.00	0 - 100	0.013
IV	5	0	0.00	1.73	5.70	0 - 40	0.092
V	6	1	16.67	1.80	5.30	0 - 33.3	0.002
VI	3	0	0.00	1.34	6.60	0 - 66.7	0.042
VII	0	0	0.00	0.00	0.00	0 - 0	1.000
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Biome	Glareolidae			Monte Carlo Analysis			
	sp	sp	(BSI=1)	Mean %	S.d.	Range	p
I	4	0	0.00	2.00	7.00	0 - 75	0.085
II	14	2	14.29	8.88	6.60	0 - 42.9	0.100
III/III	11	0	0.00	4.41	5.60	0 - 27.3	0.728
III	6	0	0.00	2.42	6.10	0 - 33.3	0.163
IV	5	0	0.00	2.30	6.60	0 - 60	0.126
V	0	0	0.00	0.00	0.00	0 - 0	1.000
VI	1	0	0.00	1.70	13.00	0 - 100	0.017
VII	4	1	25.00	1.95	6.80	0 - 50	0.001
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Biome	Alcidae			Monte Carlo Analysis			
	sp	sp	(BSI=1)	Mean %	S.d.	Range	p
I	0	0	0.00	0.00	0.00	0 - 0	1.000
II	0	0	0.00	0.00	0.00	0 - 0	1.000
III/III	0	0	0.00	0.00	0.00	0 - 0	1.000
III	2	1	50.00	3.04	12.00	0 - 100	0.001
IV	2	0	0.00	3.00	12.00	0 - 100	0.063
V	1	0	0.00	2.78	16.00	0 - 100	0.029
VI	11	0	0.00	5.19	6.10	0 - 27.3	0.891
VII	0	0	0.00	0.00	0.00	0 - 0	1.000
VIII	14	0	0.00	7.16	5.90	0 - 28.6	<0.001
IX	18	5	27.78	14.40	6.50	0 - 38.9	0.006

Figure 2-figure supplement 1K. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Turnicidae, Glareolidae and Alcidae.

2. Biomic specialization

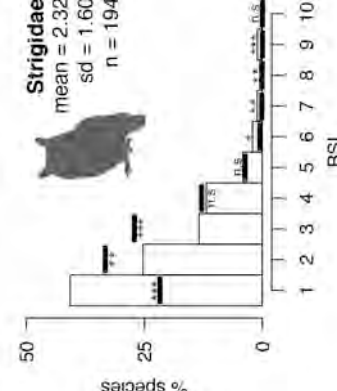
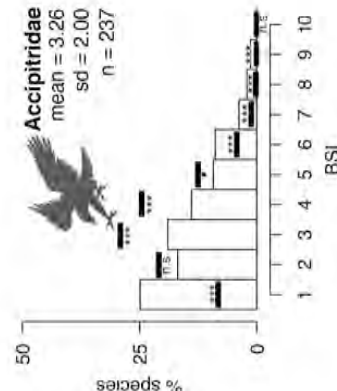
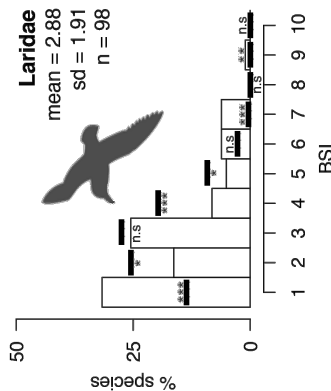


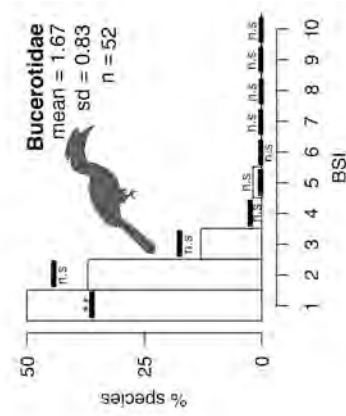
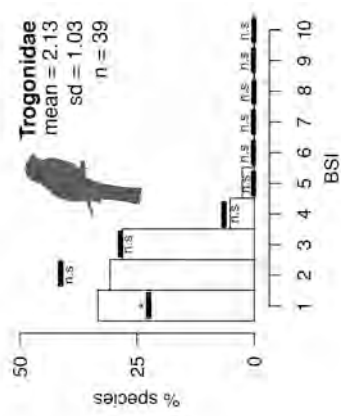
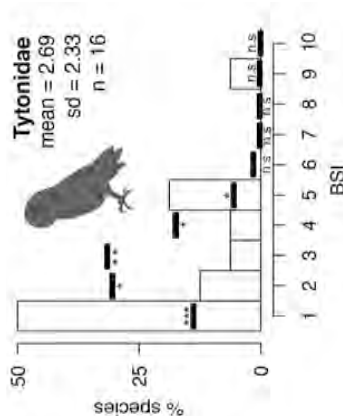
Figure 2-figure supplement 1L. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Laridae, Accipitridae and Strigidae.

BSI		Monte Carlo Analysis					Biome		Monte Carlo Analysis					
	%	Mean %	S.d.	Range	p			sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	31.60	14.00	3.00	4.3 - 24	<0.001	I	29	1	3.45	4.59	3.80	0 - 20.7	0.655	
2	16.30	26.00	4.10	10 - 41	0.013	II	34	2	5.88	5.03	3.70	0 - 23.5	0.320	
3	25.50	28.00	4.60	12 - 44	0.464	III/II	22	0	0.00	4.2	4.10	0 - 22.7	<0.001	
4	8.16	20.00	3.80	6.3 - 34	<0.001	III	26	8	30.77	4.47	4.00	0 - 19.2	<0.001	
5	5.10	9.30	2.70	1.1 - 21	0.035	IV	27	1	3.70	4.36	3.90	0 - 22.2	0.495	
6	6.12	3.10	1.70	0 - 11	0.057	V	31	1	3.23	4.74	3.60	0 - 22.6	0.789	
7	6.12	0.68	0.82	0 - 5.3	<0.001	VI	40	1	2.50	5.42	3.50	0 - 20	0.114	
8	0.00	0.11	0.33	0 - 3.2	0.904	VII	31	6	19.35	4.79	3.70	0 - 22.6	<0.001	
9	1.02	0.01	0.09	0 - 1.1	0.007	VIII	20	1	5.00	4.01	4.30	0 - 25	0.235	
10	0.00	0.00	0.02	0 - 1.1	1.000	IX	22	10	45.45	4.19	4.20	0 - 22.7	<0.001	

BSI		%	Monte Carlo Analysis					Biome		Accipitridae			Monte Carlo Analysis			
			Mean %	S.d.	Range	p	sp			sp (BSI=1)	%	Mean %	S.d.	Range	p	
1	24.90	8.10	1.60	3 - 14	<0.001	I	144	39	27.08	3.34	1.40	0 - 9.72	<0.001			
2	16.90	21.00	2.30	12 - 30	0.053	II	137	4	2.92	3.11	1.40	0 - 9.49	0.739			
3	19.00	29.00	2.90	18 - 41	<0.001	II/III	112	3	2.68	2.46	1.40	0 - 8.93	0.416			
4	13.90	24.00	2.70	15 - 35	<0.001	III	47	0	0.00	1.64	1.80	0 - 10.6	<0.001			
5	9.28	13.00	1.90	5.6 - 21	0.028	IV	57	1	1.75	1.76	1.70	0 - 10.5	0.361			
6	8.86	4.30	1.20	0.85 - 9.9	<0.001	V	108	3	2.78	2.40	1.40	0 - 9.26	0.348			
7	3.80	0.91	0.60	0 - 3.8	<0.001	VI	51	0	0.00	1.70	1.80	0 - 13.7	<0.001			
8	2.11	0.11	0.21	0 - 1.3	<0.001	VII	61	7	11.48	1.78	1.70	0 - 11.5	<0.001			
9	1.27	0.01	0.06	0 - 0.86	<0.001	VIII	43	1	2.33	1.60	1.90	0 - 11.6	0.178			
10	0.00	0.00	0.01	0 - 0.43	0.999	IX	12	1	8.33	1.33	3.30	0 - 25	0.010			

Monte Carlo Analysis										Strigidae				Monte Carlo Analysis			
BSI		%		Monte Carlo Analysis				Biome		Strigidae		Monte Carlo Analysis					
		Mean %	S.d.	Range				sp	sp	(BSI=I)	%	Mean %	S.d.	Range	p		
1	40.70	22.00	2.40	13 - 30	<0.001	I	98	41	41.84	11.00	2.90	2.04 - 22.4	<0.001				
2	25.30	33.00	3.40	21 - 45	0.007	II	98	18	18.37	11.00	2.90	2.04 - 23.5	0.006				
3	13.40	27.00	3.20	15 - 39	<0.001	III/II	41	2	4.88	6.91	3.80	0 - 24.4	0.258				
4	11.90	13.00	2.20	5.4 - 22	0.439	III	21	1	4.76	6.20	5.20	0 - 28.6	0.605				
5	4.12	3.80	1.30	0 - 10	0.632	IV	21	0	0.00	6.08	5.10	0 - 28.6	<0.001				
6	2.06	0.69	0.60	0 - 3.9	0.036	V	76	14	18.42	8.96	3.10	0 - 22.4	0.001				
7	1.03	0.07	0.20	0 - 1.7	0.008	VI	38	0	0.00	6.66	4.00	0 - 23.7	<0.001				
8	0.52	0.01	0.05	0 - 0.56	0.009	VII	19	0	0.00	5.92	5.30	0 - 31.6	<0.001				
9	1.03	0.00	0.01	0 - 0.57	<0.001	VIII	36	2	5.56	6.70	4.10	0 - 25	0.782				
10	0.00	0.00	0.00	0 - 0	1.000	IX	3	1	33.33	5.62	13.00	0 - 66.7	0.009				

2. Biomic specialization



BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	50.00	14.00	7.20	0 - 44	<0.001
2	12.50	30.00	11.00	0 - 69	0.024
3	6.25	31.00	12.00	0 - 80	0.003
4	6.25	18.00	8.50	0 - 50	0.030
5	18.80	5.70	5.30	0 - 29	0.016
6	0.00	1.10	2.60	0 - 14	0.837
7	0.00	0.12	0.89	0 - 13	0.981
8	0.00	0.01	0.20	0 - 6.7	0.999
9	6.25	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Tytonidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	12	6	50.00	8.92	7.30	0 - 41.7	<0.001
II	9	1	11.11	4.93	6.70	0 - 33.3	0.056
III/III	3	0	0.00	2.74	9.40	0 - 66.7	0.088
IV	1	0	0.00	2.15	15.00	0 - 100	0.022
V	2	0	0.00	2.46	11.00	0 - 100	0.051
VI	7	1	14.29	3.89	7.00	0 - 57.1	0.020
VII	3	0	0.00	2.58	9.00	0 - 66.7	0.083
VIII	3	0	0.00	2.66	9.20	0 - 66.7	0.085
IX	0	0	0.00	2.79	9.50	0 - 66.7	0.089
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	33.30	23.00	5.00	5.4 - 44	0.010
2	30.80	41.00	7.80	11 - 68	0.086
3	28.20	29.00	6.20	7.7 - 53	0.729
4	5.13	6.6	3.40	0 - 26	0.291
5	2.56	0.36	0.95	0 - 5.7	0.124
6	0.00	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

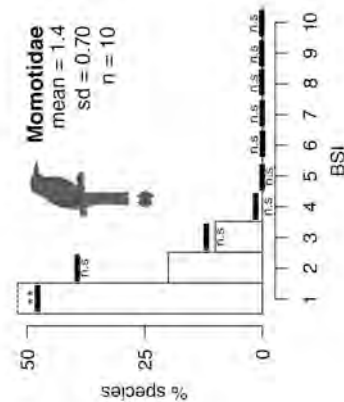
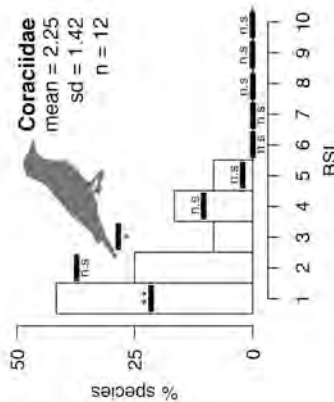
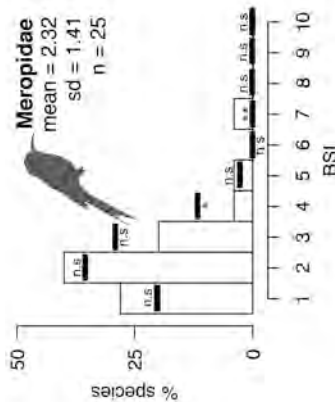
Biome	Trogonidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	30	10	33.33	15.70	5.10	0 - 36.7	<0.001
II	20	2	10.00	7.48	5.00	0 - 30	0.195
III/III	3	0	0.00	3.89	8.90	0 - 100	0.126
IV	0	0	0.00	0.00	0.00	0 - 0	1.000
V	22	1	4.55	8.22	4.80	0 - 31.8	0.128
VI	0	0	0.00	0.00	0.00	0 - 0	1.000
VII	0	0	0.00	0.00	0.00	0 - 0	1.000
VIII	8	0	0.00	4.60	7.20	0 - 50	0.470
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	50.00	37.00	5.20	19 - 54	0.004
2	36.50	44.00	7.00	13 - 67	0.162
3	11.50	16.00	4.50	2 - 32	0.169
4	0.00	2.20	2.00	0 - 11	0.319
5	1.92	0.12	0.50	0 - 4.5	0.060
6	0.00	0.00	0.078	0 - 2.2	0.999
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Bucerotidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	33	18	54.55	24.30	5.70	6.06 - 45.5	<0.001
II	32	7	21.88	23.00	5.70	6.25 - 46.9	0.872
III/III	10	1	10.00	11.20	9.60	0 - 50	0.458
IV	2	0	0.00	8.99	20.0	0 - 100	0.210
V	8	0	0.00	10.70	11.00	0 - 82.5	<0.001
VI	0	0	0.00	0.00	0.00	0 - 0	1.000
VII	1	0	0.00	9.04	29.00	0 - 100	0.0994
VIII	1	0	0.00	9.60	29.00	0 - 100	0.106
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Figure 2-figure supplement 1M. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Tytonidae, Trogonidae and Bucerotidae.

2. Biomic specialization



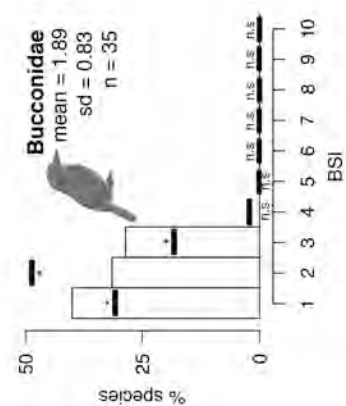
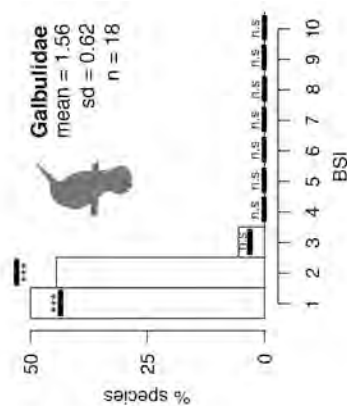
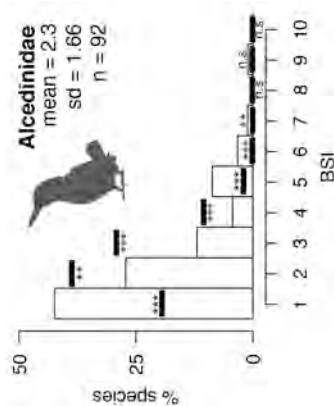
Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Meropidae			p
						Biome	sp	sp (BSI=1)	
I	28.00	20.00	6.40	0 - 44	0.105	I	14	4	28.57
II	40.00	36.00	9.40	0 - 75	0.407	II	17	2	11.76
III	20.00	29.00	8.80	0 - 70	0.127	III/III	11	0	0.00
IV	4.00	12.00	5.70	0 - 38	0.027	IV	4	0	0.00
V	4.00	2.60	3.00	0 - 17	0.622	V	4	0	0.00
VI	0.00	0.31	1.10	0 - 9.1	0.928	VI	4	1	25.00
VII	4.00	0.02	0.28	0 - 5	0.003	VII	2	0	0.00
VIII	0.00	0.00	0.06	0 - 4.3	1.000	VIII	2	0	0.00
IX	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00
X	0.00	0.00	0.00	0 - 0	1.000				

Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Coraciidae			p
						Biome	sp	sp (BSI=1)	
I	41.70	22.00	9.50	0 - 50	0.004	I	6	2	33.33
II	25.00	37.00	14.00	0 - 83	0.148	II	9	3	33.33
III	8.33	28.00	12.00	0 - 80	0.016	III/III	5	0	0.00
IV	16.70	10.00	7.80	0 - 40	0.250	IV	1	0	0.00
V	8.33	2.10	4.00	0 - 20	0.128	V	1	0	0.00
VI	0.00	0.21	1.40	0 - 10	0.976	VI	2	0	0.00
VII	0.00	0.01	0.32	0 - 10	0.999	VII	2	0	0.00
VIII	0.00	0.00	0.09	0 - 9.1	1.000	VIII	1	0	0.00
IX	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00
X	0.00	0.00	0.00	0 - 0	1.000				

Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Momotidae			p
						Biome	sp	sp (BSI=1)	
I	70.00	48.00	14.00	0 - 80	0.007	I	6	4	66.67
II	20.00	39.00	16.00	0 - 100	0.099	II	4	2	50.00
III	10.00	12.00	10.00	0 - 67	0.417	III/III	1	0	0.00
IV	0.00	1.50	4.20	0 - 29	0.882	IV	0	0	0.00
V	0.00	0.08	1.00	0 - 17	0.994	V	0	0	0.00
VI	0.00	0.00	0.00	0 - 0	1.000	VI	2	1	50.00
VII	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
VIII	0.00	0.00	0.00	0 - 0	1.000	VIII	0	0	0.00
IX	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00
X	0.00	0.00	0.00	0 - 0	1.000				

Figure 2-figure supplement 1N. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Meropidae, Coraciidae and Momotidae.

2. Biomic specialization



Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	42.40	20.00	3.20	8 - 31	<0.001	I	76	32	42.11
2	27.20	39.00	4.90	20 - 58	0.009	II	55	5	9.09
3	12.00	29.00	4.40	12 - 47	<0.001	III/III	24	0	0.00
4	4.35	10.00	2.70	2.2 - 22	0.005	III	4	0	0.00
5	8.70	1.90	1.30	0 - 8.9	0.000	IV	9	0	0.00
6	3.26	0.18	0.44	0 - 3.4	0.000	V	27	2	7.41
7	1.09	0.01	0.10	0 - 1.2	0.007	VI	10	0	0.00
8	0.00	0.00	0.02	0 - 1.1	1.000	VII	5	0	0.00
9	1.09	0.00	0.00	0 - 0	1.000	VIII	2	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	50.00	44.00	5.00	35 - 50	<0.001	I	17	8	47.06
2	44.40	54.00	6.80	44 - 65	<0.001	II	10	1	10.00
3	5.56	3.00	2.90	0 - 5.9	0.325	III/III	1	0	0.00
4	0.00	0.00	0.00	0 - 0	1.000	III	0	0	0.00
5	0.00	0.00	0.00	0 - 0	1.000	IV	0	0	0.00
6	0.00	0.00	0.00	0 - 0	1.000	V	0	0	0.00
7	0.00	0.00	0.00	0 - 0	1.000	VI	0	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
9	0.00	0.00	0.00	0 - 0	1.000	VIII	0	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

Monte Carlo Analysis					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	40.00	31.00	4.90	12 - 49	0.014	I	33	13	39.39
2	31.40	49.00	8.20	17 - 82	0.011	II	19	1	5.26
3	28.60	19.00	4.90	0 - 36	0.019	III/III	4	0	0.00
4	0.00	2.00	2.20	0 - 12	0.459	III	0	0	0.00
5	0.00	0.04	0.35	0 - 3	0.985	IV	0	0	0.00
6	0.00	0.00	0.00	0 - 0	1.000	V	9	0	0.00
7	0.00	0.00	0.00	0 - 0	1.000	VI	0	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
9	0.00	0.00	0.00	0 - 0	1.000	VIII	1	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

Figure 2-figure supplement 10. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Alcedinidae, Galbulidae and Bucconidae.

2. Biomic specialization

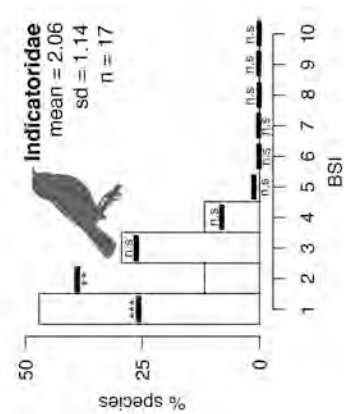
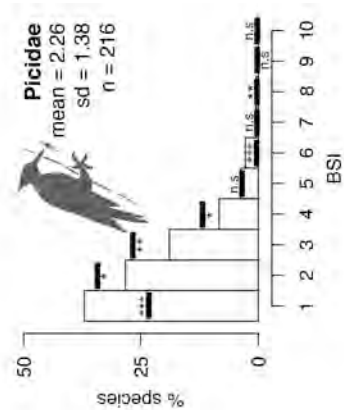
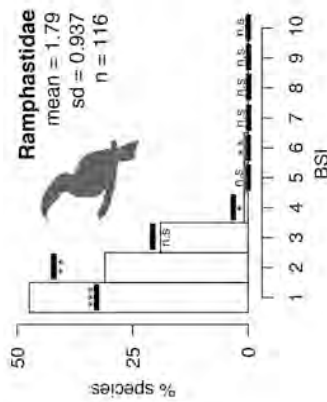


Figure 2-figure supplement 1P. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Ramphastidae, Picidae and Indicatoridae.

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range	p	Biome	Ramphastidae
I	47.40	33.00	3.40	22 - 45	<0.001	I	sp 69 sp (BSI=1) 25
2	31.00	42.00	4.70	25 - 58	0.008	II	66 18
3	19.00	21.00	3.30	10 - 33	0.390	III/III	12 1
4	0.86	3.40	1.60	0 - 11	0.015	IV	2 0
5	0.86	0.21	0.44	0 - 2.9	0.261	V	1 0
6	0.86	0.01	0.08	0 - 0.98	0.007	VI	49 9
7	0.00	0.00	0.00	0 - 0	1.000	VII	1 0
8	0.00	0.00	0.00	0 - 0	1.000	VIII	2 0
9	0.00	0.00	0.00	0 - 0	1.000	IX	6 2
10	0.00	0.00	0.00	0 - 0	1.000		0 0

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range	p	Biome	Picidae
1	37.00	23.00	2.30	15 - 32	<0.001	I	sp 115 sp (BSI=1) 41
2	28.20	34.00	3.20	21 - 47	0.035	II	102 16
3	19.00	27.00	3.00	17 - 38	0.004	III/III	44 5
4	8.33	12.00	2.00	5 - 21	0.032	IV	12 3
5	3.70	3.30	1.20	0 - 8.2	0.538	V	16 1
6	2.78	0.54	0.50	0 - 2.9	<0.001	VI	82 8
7	0.46	0.06	0.17	0 - 1.5	0.121	VII	35 1
8	0.46	0.00	0.04	0 - 0.51	0.006	VIII	37 2
9	0.00	0.00	0.00	0 - 0	1.000	IX	43 3
10	0.00	0.00	0.00	0 - 0	1.000		2 0

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range	p	Biome	Indicatoridae
1	47.10	26.00	8.50	0 - 53	0.002	I	sp 9 sp (BSI=1) 5
2	11.80	39.00	12.00	0 - 82	0.005	II	10 2
3	29.40	26.00	9.90	0 - 64	0.528	III/III	4 0
4	11.80	8.10	6.00	0 - 43	0.464	IV	0 0
5	0.00	1.10	2.60	0 - 20	0.828	V	2 0
6	0.00	0.08	0.70	0 - 7.7	0.988	VI	8 1
7	0.00	0.00	0.07	0 - 7.1	1.000	VII	0 0
8	0.00	0.00	0.00	0 - 0	1.000	VIII	1 0
9	0.00	0.00	0.00	0 - 0	1.000	IX	1 0
10	0.00	0.00	0.00	0 - 0	1.000		0 0

2. Biomic specialization

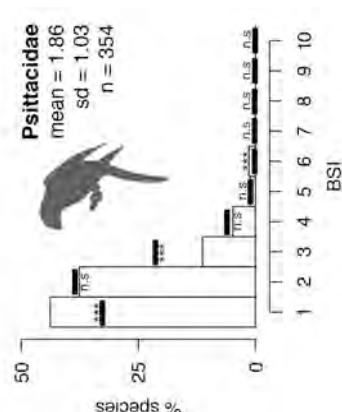
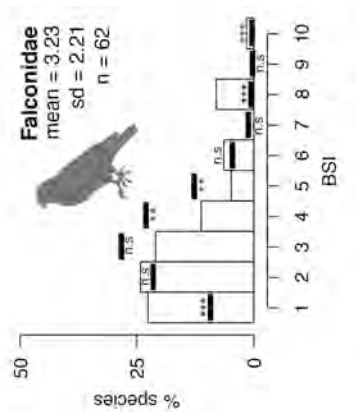


Figure 2-figure supplement 1Q. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species. in this plate: Falconidae and Psittacidae.

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	22.60	9.10	3.20	0 - 23	<0.001	2.86	3.20	0 - 19.2	<0.001
2	24.20	21.00	4.60	6.6 - 37	0.329	4.12	3.10	0 - 16.2	0.228
3	21.00	28.00	5.80	6.7 - 52	0.104	2.91	3.10	0 - 17.9	0.240
4	11.30	23.00	5.20	6.6 - 44	0.005	2.41	3.50	0 - 21.1	0.009
5	4.84	13.00	3.80	0 - 28	0.006	2.20	3.70	0 - 26.7	0.042
6	6.45	4.60	2.50	0 - 15	0.325	2.43	3.30	0 - 23.8	0.703
7	0.00	1.10	1.30	0 - 8.3	0.494	2.29	3.60	0 - 23.5	0.496
8	8.06	0.17	0.52	0 - 4.9	<0.001	2.27	3.60	0 - 23.5	0.005
9	0.00	0.01	0.14	0 - 1.7	0.993	2.15	3.90	0 - 28.6	0.356
10	1.61	0.00	0.04	0 - 1.7	<0.001	1.80	5.40	0 - 50	0.004

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	43.80	33.00	2.00	23 - 40	<0.001	21.70	2.40	12.6 - 31.1	<0.001
2	37.60	39.00	2.70	29 - 50	0.540	17.30	2.50	8.33 - 26.2	0.386
3	11.30	21.00	2.10	14 - 30	<0.001	10.70	4.10	0 - 27.8	0.420
4	4.80	6.20	1.20	2.4 - 11	0.123	9.64	6.80	0 - 44.4	0.093
5	1.13	1.10	0.55	0 - 3.7	0.787	10.00	5.10	0 - 32.4	<0.001
6	1.41	0.10	0.18	0 - 1.2	<0.001	12.70	3.20	1.98 - 25.7	0.092
7	0.00	0.01	0.04	0 - 0.32	0.983	9.92	5.40	0 - 37.9	0.061
8	0.00	0.00	0.01	0 - 0.31	1.000	9.28	9.60	0 - 55.6	<0.001
9	0.00	0.00	0.00	0 - 0	1.000	10.20	4.90	0 - 36.1	0.370
10	0.00	0.00	0.00	0 - 0	1.000	9.12	14.00	0 - 100	0.464

2. Biomic specialization

Appendix 2.8.4. Supplementary data of Figure 2 (Fig. S2 from A to O) – Non migratory species (fam > 10 spp)

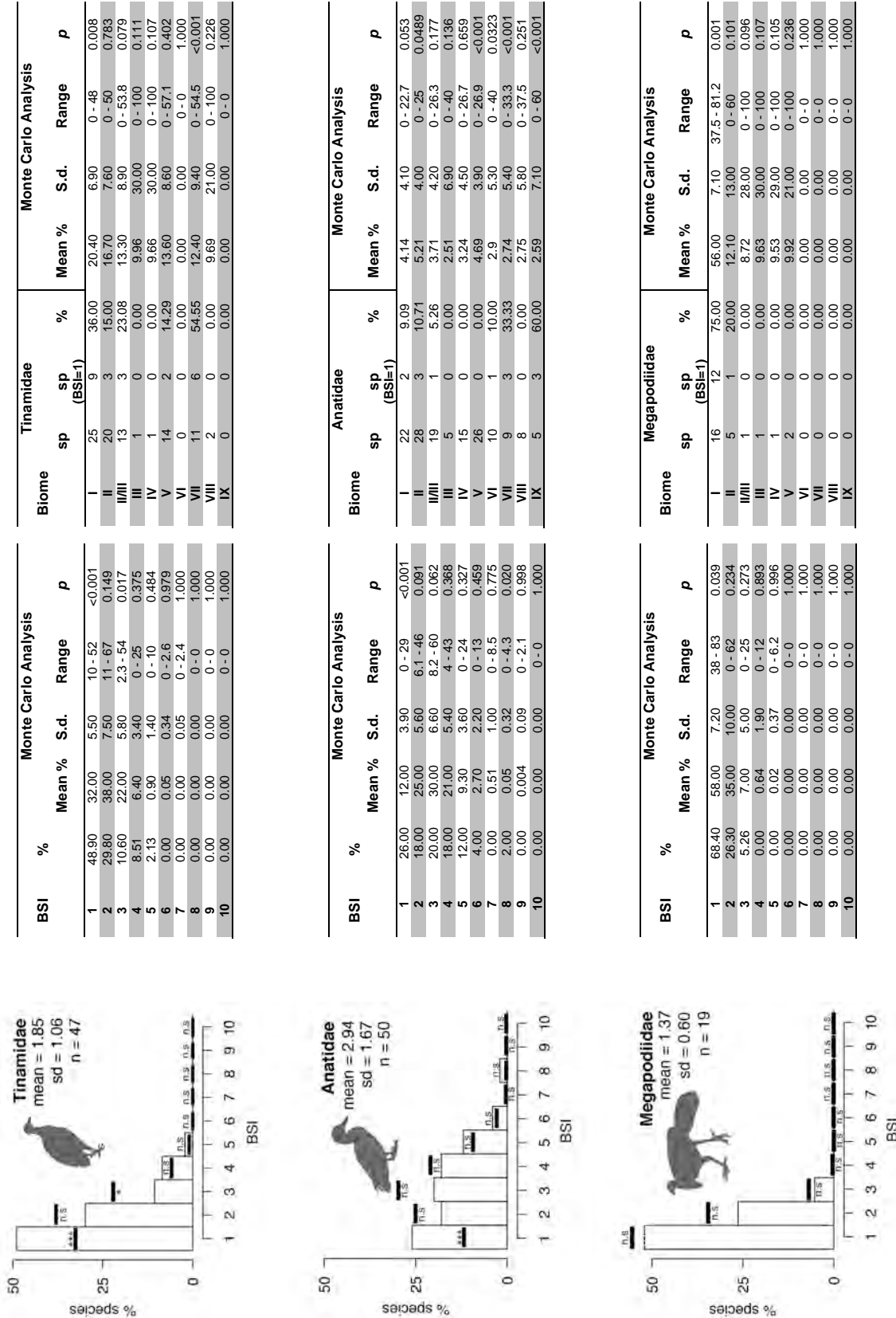
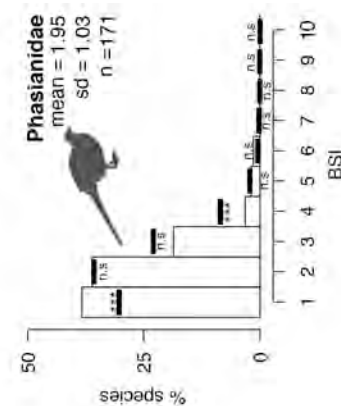
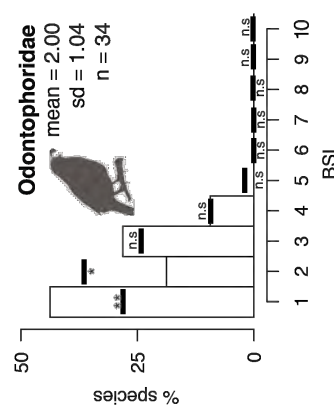
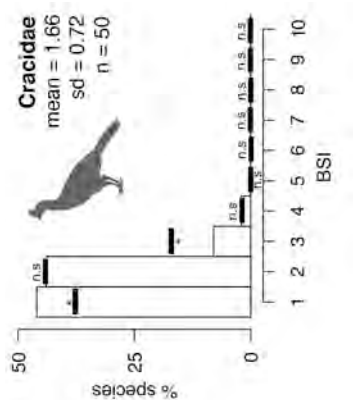


Figure 2-figure supplement 2A. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Tinamidae, Anatidae and Megapodiidae.

2. Biomic specialization



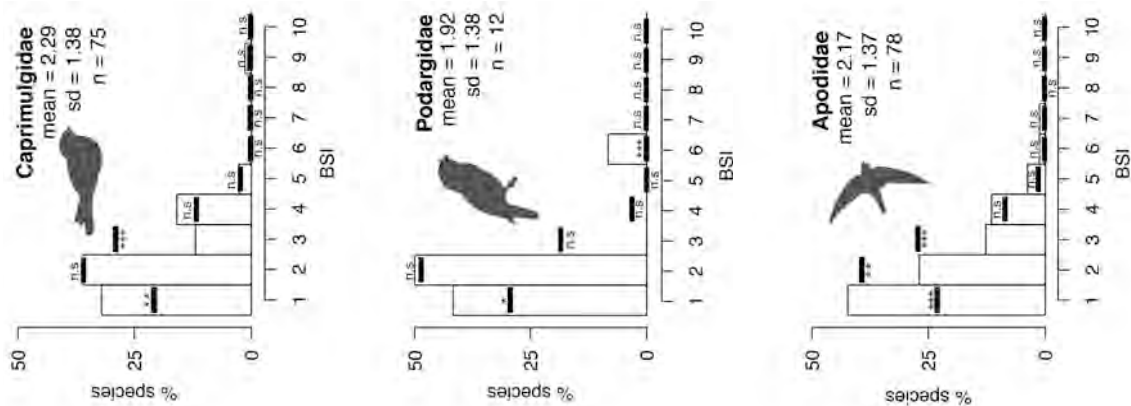
Monte Carlo Analysis						Monte Carlo Analysis							
BSI	%	Mean %	S.d.	Range	p	Biome	Cracidae						
							sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	46.00	38.00	5.30	17 - 56	0.049	I	33	10	30.30	27.10	5.80	6.06 - 48.5	0.261
2	44.00	43.00	7.20	17 - 68	0.866	II	27	9	33.33	20.10	6.20	0 - 44.4	0.008
3	8.00	17.00	4.60	2.1 - 37	0.015	III/III	4	0	0.00	10.10	15.00	0 - 75	0.530
4	2.00	1.90	1.80	0 - 10	0.641	III	0	0	0.00	0.00	0.00	0 - 0	1.000
5	0.00	0.06	0.36	0 - 4.4	0.973	IV	0	0	0.00	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000	V	16	4	25.00	13.40	7.80	0 - 50	0.039
7	0.00	0.00	0.00	0 - 0	1.000	VI	0	0	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000	VIII	3	0	0.00	9.87	17.00	0 - 100	0.366
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00	0.00	0.00	0 - 0	1.000

BSI		Monte Carlo Analysis					Biome			Odontophoridae		Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p		sp	sp (BSI=1)	%	Mean %	S.d.	Range	p			
1	44.10	29	6.30	7.1 - 53	0.005	I	14	7	50.00	14.30	8.60	0 - 53.8	<0.001			
2	20.60	37	8.60	9.4 - 66	0.030	II	14	3	21.43	14.30	8.60	0 - 46.2	0.120			
3	26.5	24	7.00	3.1 - 54	0.511	III/II	4	0	0.00	9.34	15.00	0 - 100	0.480			
4	8.82	8.6	4.50	0 - 30	0.890	III	3	1	33.33	9.01	16.00	0 - 100	0.023			
5	0.00	1.9	2.30	0 - 15	0.535	IV	2	0	0.00	8.71	20.00	0 - 100	0.201			
6	0.00	0.25	0.88	0 - 7.1	0.926	V	17	4	23.53	16.70	8.00	0 - 52.9	0.126			
7	0.00	0.02	0.23	0 - 3.7	0.995	VI	4	0	0.00	9.33	14.00	0 - 75	0.483			
8	0.00	0.00	0.064	0 - 3.2	1.000	VII	3	0	0.00	8.99	16.00	0 - 100	0.329			
9	0.00	0.00	0.00	0 - 0	1.000	VIII	7	0	0.00	10.40	11.00	0 - 71.4	<0.001			
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00	0.00	0.00	0 - 0	1.000			

Monte Carlo Analysis						Monte Carlo Analysis								
BSI		%	Monte Carlo Analysis			Biome		Phasianidae		Monte Carlo Analysis				
			Mean %	S.d.	Range	p		sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1		39.80	31.00	2.90	20 - 42	<0.001	I	46	16	34.78	13.10	4.70	0 - 34.8	<0.001
2		35.10	36.00	3.90	22 - 53	0.751	II	86	21	24.42	19.40	3.80	7 - 34.9	0.077
3		19.30	23.00	3.10	11 - 36	0.174	III/III	34	1	2.94	12.00	5.40	0 - 35.3	0.011
4		2.92	8.50	2.00	1.8 - 16	<0.001	III	9	3	33.33	10.30	10.00	0 - 55.6	0.010
5		1.75	2.00	1.10	0 - 7.6	0.616	IV	13	0	0.00	10.40	8.40	0 - 53.8	<0.001
6		1.17	0.29	0.43	0 - 3.3	0.078	V	51	5	9.80	13.80	4.60	0 - 33.3	0.158
7		0.00	0.03	0.13	0 - 1.3	0.961	VI	34	2	5.88	12.10	5.40	0 - 35.3	0.071
8		0.00	0.00	0.03	0 - 0.7	0.998	VII	37	16	43.24	12.40	5.20	0 - 37.8	<0.001
9		0.00	0.00	0.00	0 - 0	1.000	VIII	22	3	13.64	10.90	6.50	0 - 40.9	0.257
10		0.00	0.00	0.00	0 - 0	1.000	IX	2	1	50.00	9.54	24.00	0 - 100	0.007

Figure 2-figure supplement 2B. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Craciidae, Odontophoridae and Phasianidae.

2. Biomic specialization



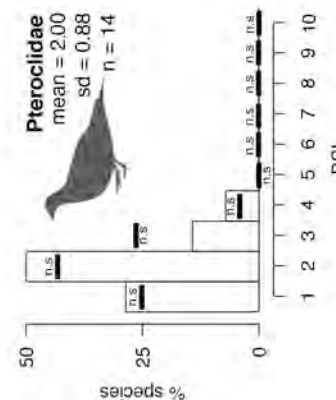
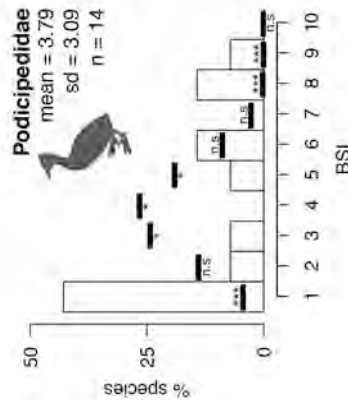
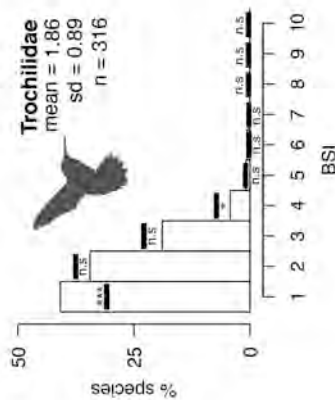
BSI	Monte Carlo Analysis				Caprimulgidae				Monte Carlo Analysis			
	%	Mean %	S.d.	Range		sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	32.00	21.00	3.80	7.4 - 34	I	43	10	23.26	10.10	4.10	0 - 27.9	<0.001
2	36.00	36.00	5.40	16 - 57	II	47	8	17.02	11.60	4.10	0 - 27.7	0.065
3	12.00	29.00	5.00	11 - 48	III/IIII	27	4	14.81	6.87	4.60	0 - 29.6	0.029
4	16.00	12.00	3.20	1.4 - 23	III	4	0	0.00	4.45	10.00	0 - 75	0.206
5	2.67	2.40	1.70	0 - 9.9	IV	4	0	0.00	4.55	10.00	0 - 75	0.206
6	0.00	0.25	0.58	0 - 4.3	V	30	1	3.33	7.17	4.50	0 - 30	0.103
7	0.00	0.01	0.14	0 - 2.9	VI	3	0	0.00	4.54	12.00	0 - 66.7	0.151
8	0.00	0.00	0.02	0 - 1.5	VII	5	1	20.00	4.69	9.50	0 - 80	0.020
9	1.33	0.00	0.00	0 - 0	VIII	9	0	0.00	4.93	7.10	0 - 44.4	0.584
10	0.00	0.00	0.00	0 - 0	IX	0	0	0.00	0.00	0.00	0 - 0	1.000

BSI	Monte Carlo Analysis				Podargidae				Monte Carlo Analysis			
	%	Mean %	S.d.	Range		sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	41.70	29.00	8.70	0 - 50	I	11	5	45.45	27.00	8.50	0 - 45.5	<0.001
2	50.00	49.00	14.00	8.3 - 92	II	7	0	0.00	5.40	6.90	0 - 14.3	0.608
3	0.00	18.00	9.20	0 - 45	III/IIII	1	0	0.00	2.50	16.00	0 - 100	0.026
4	0.00	3.20	4.60	0 - 18	III	1	0	0.00	2.77	16.00	0 - 100	0.029
5	0.00	0.31	1.60	0 - 9.1	IV	1	0	0.00	2.42	15.00	0 - 100	0.025
6	8.33	0.01	0.32	0 - 9.1	V	1	0	0.00	2.25	15.00	0 - 100	0.023
7	0.00	0.00	0.09	0 - 9.1	VI	1	0	0.00	2.40	15.00	0 - 100	0.025
8	0.00	0.00	0.00	0 - 0	VII	0	0	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	IX	0	0	0.00	0.00	0.00	0 - 0	1.000

BSI	Monte Carlo Analysis				Apodidae				Monte Carlo Analysis			
	%	Mean %	S.d.	Range		sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	42.30	23.00	3.70	8.2 - 37	I	55	19	34.55	14.70	3.90	1.82 - 32.7	<0.001
2	26.90	39.00	5.40	19 - 62	II	48	6	12.50	11.30	3.90	0 - 27.1	0.374
3	12.80	27.00	4.70	11 - 46	III/IIII	14	1	7.14	5.32	5.90	0 - 42.9	0.203
4	11.50	8.70	2.80	0 - 21	III	4	1	25.00	4.60	10.00	0 - 75	0.012
5	3.85	1.40	1.30	0 - 7	IV	5	0	0.00	4.57	9.20	0 - 60	0.268
6	1.28	0.13	0.40	0 - 2.8	V	28	5	17.86	6.80	4.50	0 - 28.6	0.006
7	1.28	0.01	0.10	0 - 1.4	VI	2	0	0.00	4.42	15.00	0 - 100	0.094
8	0.00	0.00	0.01	0 - 1.3	VII	7	1	14.29	4.71	7.90	0 - 42.9	0.038
9	0.00	0.00	0.00	0 - 0	VIII	6	0	0.00	4.64	8.50	0 - 50	0.333
10	0.00	0.00	0.00	0 - 0	IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Figure 2-figure supplement 2C. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Caprimulgidae, Podargidae and Apodidae.

2. Biomic specialization



Monte Carlo Analysis					Trochilidae				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	41.80	32.00	2.10	24 - 41	<0.001	I	157	41	26.11
2	35.10	38.00	2.80	29 - 50	0.149	II	123	21	17.07
3	19.00	22.00	2.20	14 - 30	0.084	III/II	29	2	6.90
4	3.48	6.40	1.30	2.4 - 11	0.009	IV	7	3	42.86
5	0.63	0.89	0.54	0 - 3.5	0.363	V	0	0	0.00
6	0.00	0.05	0.14	0 - 1.1	0.858	VI	146	33	22.60
7	0.00	0.001	0.02	0 - 0.35	0.998	VII	0	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VIII	58	26	44.83
9	0.00	0.00	0.00	0 - 0	1.000	IX	68	6	8.82
10	0.00	0.00	0.00	0 - 0	1.000		0	0	0.00

Monte Carlo Analysis					Podicipedidae				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	42.90	4.70	5.20	0 - 29	<0.001	I	4	0	0.00
2	7.14	14.00	8.10	0 - 50	0.105	II	5	1	20.00
3	7.14	24.00	11.00	0 - 71	0.019	III/II	7	0	0.00
4	0.00	26.00	12.00	0 - 77	0.015	IV	4	0	0.00
5	7.14	19.00	9.70	0 - 62	0.048	V	5	0	0.00
6	14.30	8.90	6.80	0 - 46	0.134	VI	8	1	12.50
7	0.00	2.80	4.10	0 - 23	0.662	VII	6	0	0.00
8	14.30	0.50	1.90	0 - 14	<0.001	VIII	8	3	37.50
9	7.14	0.06	0.65	0 - 7.7	0.001	IX	5	1	20.00
10	0.00	0.001	0.11	0 - 8.3	1.000		1	0	0.00

Monte Carlo Analysis					Pteroclididae				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	28.60	25.00	9.00	0 - 57	0.464	I	0	0	0.00
2	50.00	44.00	14.00	0 - 92	0.391	II	9	0	0.00
3	14.30	26.00	10.00	0 - 73	0.062	III/II	10	0	0.00
4	7.14	4.60	5.00	0 - 27	0.508	IV	6	2	33.33
5	0.00	0.22	1.30	0 - 9.1	0.972	V	1	0	0.00
6	0.00	0.00	0.00	0 - 0	1.000	VI	0	0	0.00
7	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VIII	2	2	100
9	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000		0	0	0.00

Figure 2-figure supplement 2D. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Trochilidae, Podicipedidae and Pteroclididae.

2. Biomic specialization

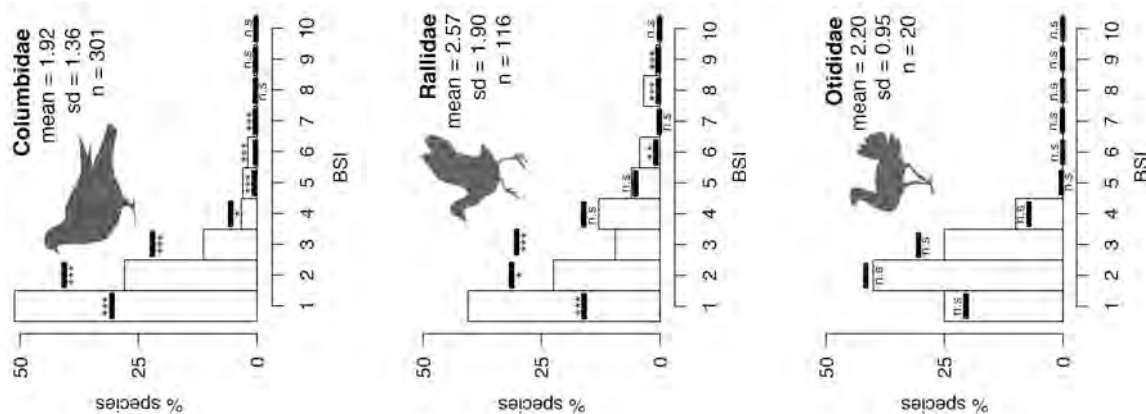


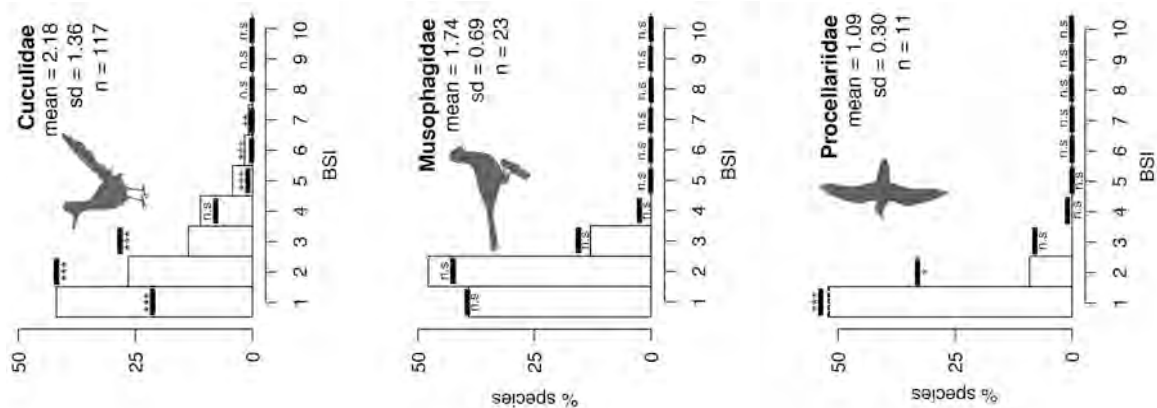
Figure 2-figure supplement 2E. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Columbidae, Rallidae and Otidae.

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range	p	Biome	Columbidae
1	51.20	31.00	2.00	23 - 38	<0.001	I	sp 209 (BSI=1) 103
2	27.90	41.00	2.90	31 - 52	<0.001	II	sp 155 (BSI=1) 35
3	11.30	22.00	2.20	14 - 30	<0.001	III/IV	sp 46 (BSI=1) 2
4	3.32	5.80	1.20	1.4 - 11	0.019	IV	sp 21 (BSI=1) 2
5	2.99	0.81	0.51	0 - 3.2	<0.001	V	sp 16 (BSI=1) 0
6	1.99	0.07	0.15	0 - 1.4	<0.001	VI	sp 85 (BSI=1) 8
7	0.66	0.00	0.03	0 - 0.37	<0.001	VII	sp 13 (BSI=1) 0
8	0.00	0.00	0.01	0 - 0.35	1.000	VIII	sp 18 (BSI=1) 4
9	0.66	0.00	0.00	0 - 0	1.000	IX	sp 12 (BSI=1) 0
10	0.00	0.00	0.00	0 - 0	1.000		sp 2 (BSI=1) 0

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range	p	Biome	Rallidae
1	40.50	16.00	2.80	5.6 - 26	<0.001	I	sp 75 (BSI=1) 24
2	22.40	32.00	4.10	16 - 48	0.015	II	sp 68 (BSI=1) 11
3	9.48	30.00	4.30	12 - 48	<0.001	III/IV	sp 31 (BSI=1) 0
4	12.90	16.00	3.10	5.3 - 30	0.175	IV	sp 8 (BSI=1) 0
5	6.03	5.00	1.90	0 - 13	0.455	V	sp 20 (BSI=1) 6
6	4.31	0.94	0.87	0 - 5.5	0.0018	VI	sp 47 (BSI=1) 1
7	0.00	0.10	0.30	0 - 2.7	0.891	VII	sp 18 (BSI=1) 4
8	3.45	0.01	0.08	0 - 0.93	<0.001	VIII	sp 12 (BSI=1) 0
9	0.86	0.00	0.02	0 - 0.89	<0.001	IX	sp 1 (BSI=1) 1
10	0.00	0.00	0.00	0 - 0	1.000		sp 1 (BSI=1) 1

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range	p	Biome	Otididae
1	25.00	20.00	6.70	0 - 50	0.233	I	sp 0 (BSI=1) 0
2	40.00	42.00	11.00	0 - 85	0.641	II	sp 10 (BSI=1) 0
3	25.00	30.00	8.80	5 - 67	0.259	III/IV	sp 17 (BSI=1) 3
4	10.00	7.20	5.00	0 - 28	0.365	IV	sp 11 (BSI=1) 1
5	0.00	0.48	1.50	0 - 11	0.909	V	sp 4 (BSI=1) 1
6	0.00	0.00	0.00	0 - 0	1.000	VI	sp 2 (BSI=1) 0
7	0.00	0.00	0.00	0 - 0	1.000	VII	sp 0 (BSI=1) 0
8	0.00	0.00	0.00	0 - 0	1.000	VIII	sp 0 (BSI=1) 0
9	0.00	0.00	0.00	0 - 0	1.000	IX	sp 0 (BSI=1) 0
10	0.00	0.00	0.00	0 - 0	1.000		sp 0 (BSI=1) 0

2. Biomic specialization



BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	41.90	21.00	2.90	8.9 - 32	<0.001
2	26.50	42.00	4.40	25 - 59	<0.001
3	13.70	28.00	3.70	16 - 42	<0.001
4	11.10	7.80	2.10	0.86 - 16	0.066
5	4.27	0.90	0.83	0 - 5.4	<0.001
6	1.71	0.05	0.21	0 - 1.8	<0.001
7	0.86	0.001	0.034	0 - 0.91	0.001
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	39.10	40.00	6.40	18 - 61	0.990
2	47.80	43.00	10.00	8.7 - 82	0.323
3	13.00	16.00	5.90	0 - 38	0.270
4	0.00	2.00	2.70	0 - 18	0.622
5	0.00	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	90.90	58.00	15.00	0 - 91	<0.001
2	9.09	33.00	16.00	0 - 100	0.029
3	0.00	7.90	9.00	0 - 60	0.493
4	0.00	0.86	3.40	0 - 33	0.940
5	0.00	0.04	0.73	0 - 17	0.998
6	0.00	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

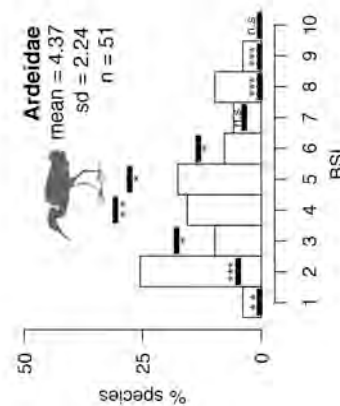
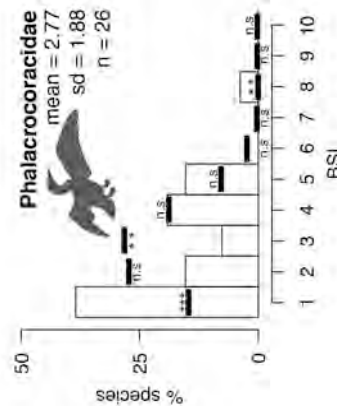
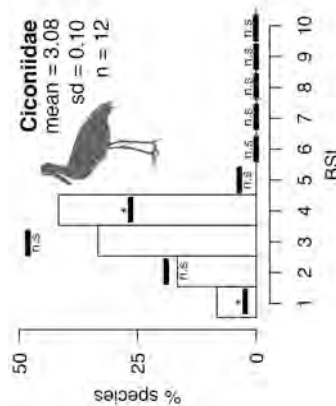
Biome	Cuculidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	93	37	39.78	15.20	2.90	4.3 - 25.8	<0.001
II	76	9	11.84	8.86	2.70	1.32 - 19.7	0.103
III/II	33	2	6.061	4.29	3.40	0 - 21.2	0.191
III	4	0	0.00	3.20	8.80	0 - 75	0.139
IV	6	0	0.00	3.23	7.20	0 - 50	0.219
V	33	1	3.03	4.37	3.40	0 - 21.2	0.762
VI	7	0	0.00	3.31	6.80	0 - 57.1	0.266
VII	2	0	0.00	3.30	13.00	0 - 100	0.070
VIII	1	0	0.00	3.26	18.00	0 - 100	0.034
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Biome	Musophagidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	6	1	16.67	4.59	8.10	0 - 33.3	0.018
II	21	7	33.33	38.00	6.50	14.3 - 61.9	0.150
III/II	6	1	16.67	4.56	8.00	0 - 33.3	0.017
III	0	0	0.00	0.00	0.00	0 - 0	1.000
IV	0	0	0.00	0.00	0.00	0 - 0	1.000
V	7	0	0.00	4.72	7.40	0 - 28.6	0.442
VI	0	0	0.00	0.00	0.00	0 - 0	1.000
VII	0	0	0.00	0.00	0.00	0 - 0	1.000
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Biome	Procellariidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	5	5	100	49.10	19.00	0 - 100	<0.001
II	1	1	100	29.50	46.00	0 - 100	<0.001
III/II	0	0	0.00	0.00	0.00	0 - 0	1.000
III	0	0	0.00	0.00	0.00	0 - 0	1.000
IV	0	0	0.00	0.00	0.00	0 - 0	1.000
V	3	2	66.67	37.00	26.00	0 - 100	0.034
VI	2	1	50.00	32.80	32.00	0 - 100	0.105
VII	1	1	100	29.40	46.00	0 - 100	<0.001
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	0	0	0.00	0.00	0.00	0 - 0	1.000

Figure 2-figure supplement 2F. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Cuculidae, Musophagidae and Procellariidae.

2. Biomic specialization



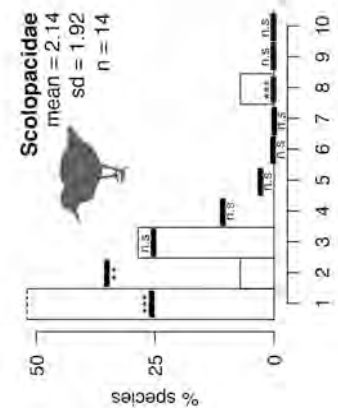
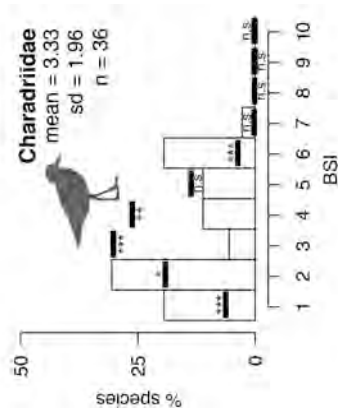
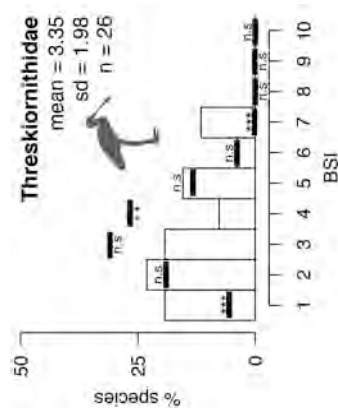
Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range			
I	8.33	2.80	4.30	0 - 17	0.022		
2	16.70	19.00	8.70	0 - 42	0.772		
3	33.30	48.00	13.00	8.3 - 92	0.086		
4	41.70	26.00	9.60	0 - 55	0.017		
5	0.00	3.50	4.70	0 - 18	0.611		
6	0.00	0.00	0.00	0 - 0	1.000		
7	0.00	0.00	0.00	0 - 0	1.000		
8	0.00	0.00	0.00	0 - 0	1.000		
9	0.00	0.00	0.00	0 - 0	1.000		
10	0.00	0.00	0.00	0 - 0	1.000		

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range			
1	38.50	15.00	5.90	0 - 38	<0.001		
2	15.40	27.00	8.20	0 - 58	0.055		
3	7.69	28.00	8.90	0 - 67	0.002		
4	19.20	19.00	7.10	0 - 43	0.792		
5	15.40	8.10	4.90	0 - 32	0.095		
6	0.00	2.40	2.90	0 - 16	0.525		
7	0.00	0.42	1.30	0 - 8.7	0.899		
8	3.85	0.05	0.45	0 - 4.5	0.010		
9	0.00	0.00	0.09	0 - 4	1.000		
10	0.00	0.00	0.00	0 - 0	1.000		

Monte Carlo Analysis				Monte Carlo Analysis			
BSI	%	Mean %	S.d.	Range			
1	3.92	0.55	1.00	0 - 5.9	0.001		
2	25.50	5.20	2.80	0 - 18	<0.001		
3	9.80	18.00	4.60	3.9 - 33	0.012		
4	15.70	31.00	6.30	7.8 - 59	0.004		
5	17.60	28.00	5.90	7.8 - 49	0.027		
6	7.84	14.00	4.10	0 - 27	0.046		
7	5.88	3.50	2.30	0 - 14	0.083		
8	9.80	0.42	0.88	0 - 5.9	<0.001		
9	3.92	0.01	0.16	0 - 2	<0.001		
10	0.00	0.00	0.00	0 - 0	1.000		

Figure 2-figure supplement 2G. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Ciconiidae, Phalacrocoracidae and Ardeidae.

2. Biomic specialization



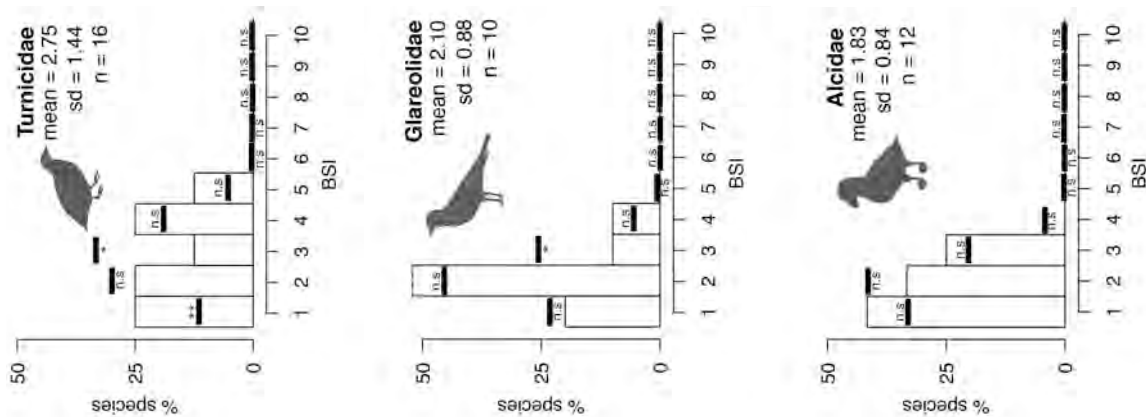
Monte Carlo Analysis						Threskiornithidae						Monte Carlo Analysis											
BSI		%				Biome		sp		(BSI=1)		sp		%		Mean %		S.d.		Range		p	
1	19.20	5.60	3.90	0 - 23	<0.001	I	12	1	8.33	0.89	2.60	0 - 16.7	0.003										
2	23.10	19.00	6.50	0 - 46	0.252	II	23	2	8.67	4.01	3.80	0 - 17.4	0.047										
3	19.20	31.00	8.80	3.8 - 65	0.063	II/III	15	0	0.00	1.05	2.60	0 - 20	0.176										
4	7.69	27.00	8.30	0 - 58	0.0025	III	6	0	0.00	0.52	2.90	0 - 33.3	0.032										
5	15.40	13.00	5.70	0 - 35	0.347	IV	8	1	12.50	0.701	2.90	0 - 25	0.001										
6	3.85	3.70	3.40	0 - 20	0.423	V	13	0	0.00	0.91	2.60	0 - 23.1	0.130										
7	11.50	0.54	1.40	0 - 12	<0.001	VI	5	1	20.00	0.53	3.30	0 - 40	<0.001										
8	0.00	0.04	0.40	0 - 4.2	0.989	VII	4	0	0.00	0.56	3.70	0 - 25	0.023										
9	0.00	<0.001	0.04	0 - 3.8	1.000	VIII	1	0	0.00	0.45	6.70	0 - 100	0.005										
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00	0.00	0.00	0 - 0	1.000										

Monte Carlo Analysis					Charadriidae					Monte Carlo Analysis				
BSI	%	Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p	
1	19.4	6.30	3.60	0 - 20	<0.001	I	13	0	0.00	1.12	2.90	0 - 23.1	0.159	
2	30.6	19.00	5.60	2.8 - 42	0.015	II	29	3	10.34	3.73	3.30	0 - 20.7	0.012	
3	5.56	30.00	7.50	2.8 - 61	<0.001	III/IIII	20	0	0.00	1.64	2.80	0 - 20	0.409	
4	11.1	26.00	7.00	2.8 - 58	0.00513	III	13	0	0.00	1.17	3.00	0 - 23.1	0.166	
5	11.1	13.00	4.90	0 - 33	0.296	IV	18	0	0.00	1.48	2.80	0 - 16.7	0.320	
6	19.4	4.00	2.90	0 - 18	<0.001	V	14	1	7.14	1.21	2.90	0 - 21.4	0.0105	
7	2.78	0.60	1.30	0 - 8.8	0.0679	VI	8	1	12.5	1.00	3.50	0 - 25	0.0022	
8	0.00	0.04	0.32	0 - 2.9	0.987	VII	4	2	50.00	0.78	4.30	0 - 25	<0.001	
9	0.00	<0.001	0.04	0 - 2.9	1.000	VIII	1	0	0.00	0.75	8.60	0 - 100	0.008	
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00	0.00	0.00	0 - 0	1.000	

Monte Carlo Analysis						Scolopacidae						Monte Carlo Analysis															
BSI		%		Mean %		S.d.		Range		p		Biome		sp		sp (BSI=1)		%		Mean %		S.d.		Range		p	
1	57.10	26.00	9.50	0 - 57	<0.001							I	4	1	25.00	9.65	14.00	0 - 75	0.041								
2	7.14	35.00	13.00	0 - 86	0.004							II	3	1	33.33	9.06	16.00	0 - 100	0.018								
3	28.60	25.00	11.00	0 - 82	0.559							III/II	1	0	0.00	7.43	26.00	0 - 100	0.080								
4	0.00	11.00	7.70	0 - 50	0.183							III	0	0	0.00	0	0.00	0 - 0	1.000								
5	0.00	2.70	4.30	0 - 30	0.682							IV	1	0	0.00	7.59	26.00	0 - 100	0.082								
6	0.00	0.46	1.90	0 - 18	0.943							V	8	3	37.50	16.1	12.00	0 - 62.5	0.012								
7	0.00	0.038	0.56	0 - 9.1	0.995							VI	3	1	33.33	8.95	16.00	0 - 100	0.015								
8	7.14	<0.001	0.083	0 - 8.3	<0.001							VII	5	1	20.00	10.8	13.00	0 - 80	0.085								
9	0.00	0.00	0.00	0 - 0	1.000							VIII	4	0	0.00	9.83	14.00	0 - 75	0.536								
10	0.00	0.00	0.00	0 - 0	1.000							IX	1	1	100	7.08	26.00	0 - 100	<0.001								

Figure 2-figure supplement 2H. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Threskiornithidae, Charadriidae and Scolopacidae.

2. Biomic specialization



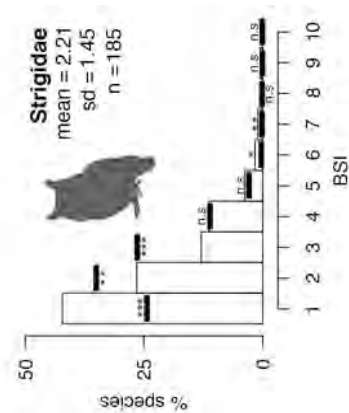
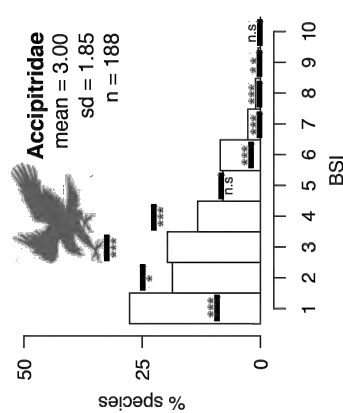
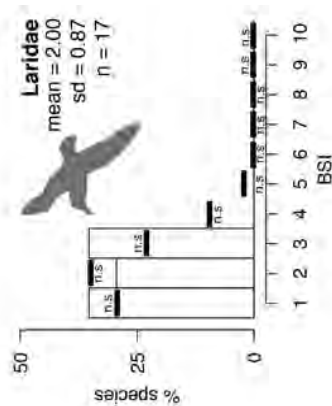
BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	25.00	12.00	6.60	0 - 38	0.010	I	6	0	0.00
2	25.00	30.00	10.00	0 - 69	0.283	II	14	2	14.29
3	12.50	33.00	12.00	0 - 80	0.014	III/II	9	1	11.11
4	25.00	19.00	8.40	0 - 50	0.199	III	1	0	0.00
5	12.50	5.30	5.00	0 - 29	0.066	IV	5	0	0.00
6	0.00	0.70	2.10	0 - 13	0.893	V	6	1	16.67
7	0.00	0.03	0.44	0 - 6.7	0.995	VI	3	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
9	0.00	0.00	0.00	0 - 0	1.000	VIII	0	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	20.00	23.00	9.60	0 - 50	0.247	I	2	0	0.00
2	60.00	45.00	15.00	0 - 90	0.134	II	9	2	22.22
3	10.00	25.00	12.00	0 - 67	0.036	III/II	6	0	0.00
4	10.00	5.70	6.50	0 - 33	0.203	III	2	0	0.00
5	0.00	0.46	2.10	0 - 11	0.956	IV	2	0	0.00
6	0.00	0.00	0.00	0 - 0	1.000	V	0	0	0.00
7	0.00	0.00	0.00	0 - 0	1.000	VI	0	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
9	0.00	0.00	0.00	0 - 0	1.000	VIII	0	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	0	0	0.00

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%
1	41.70	33	11.00	0 - 67	0.176	I	0	0	0.00
2	33.30	41	15.00	0 - 100	0.333	II	0	0	0.00
3	25.00	21	11.00	0 - 67	0.491	III/II	0	0	0.00
4	0.00	4.4	5.60	0 - 33	0.574	III	2	1	50.00
5	0.00	0.4	1.90	0 - 22	0.956	IV	1	0	0.00
6	0.00	0.013	0.34	0 - 10	0.999	V	1	0	0.00
7	0.00	0.00	0.00	0 - 0	1.000	VI	4	0	0.00
8	0.00	0.00	0.00	0 - 0	1.000	VII	0	0	0.00
9	0.00	0.00	0.00	0 - 0	1.000	VIII	5	0	0.00
10	0.00	0.00	0.00	0 - 0	1.000	IX	9	4	44.44

Figure 2-figure supplement 21. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Turnicidae, Glareolidae and Alcidae.

2. Biomic specialization



BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	35.30	30.00	9.30	0 - 59	0.360
2	29.40	35.00	12.00	0 - 80	0.499
3	35.30	23.00	10.00	0 - 62	0.147
4	0.00	9.60	6.80	0 - 42	0.170
5	0.00	2.50	3.80	0 - 25	0.665
6	0.00	0.40	1.60	0 - 15	0.941
7	0.00	0.05	0.58	0 - 8.3	0.993
8	0.00	0.01	0.12	0 - 8.3	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Laridae			Monte Carlo Analysis			
	sp	sp	(BSI=1)	Mean %	S.d.	Range	p
I	6	1	0	14.90	14.00	0 - 66.7	<0.001
II	7	1	14.29	16.50	13.00	0 - 71.4	0.474
III	4	0	0.00	12.40	16.00	0 - 75	0.733
IV	4	3	75.00	13.10	16.00	0 - 75	<0.001
V	3	0	0.00	11.40	18.00	0 - 100	0.453
VI	3	0	0.00	12.00	19.00	0 - 100	0.470
VII	3	0	0.00	12.10	18.00	0 - 100	0.482
VIII	1	0	0.00	10.50	31.00	0 - 100	0.117
IX	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	3	2	66.67	11.70	18.00	0 - 100	<0.001

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	27.70	9.20	1.80	2.7 - 17	<0.001
2	18.60	25.00	2.80	15 - 37	0.0139
3	19.70	32.00	3.40	19 - 44	<0.001
4	13.30	23.00	2.80	13 - 33	<0.001
5	7.98	8.70	1.80	2.1 - 16	0.462
6	8.51	1.90	0.95	0 - 6	<0.001
7	2.66	0.24	0.36	0 - 2.2	<0.001
8	1.06	0.017	0.09	0 - 1.1	<0.001
9	0.53	<0.001	0.02	0 - 0.55	0.001
10	0.00	0.00	0.00	0 - 0	1.000

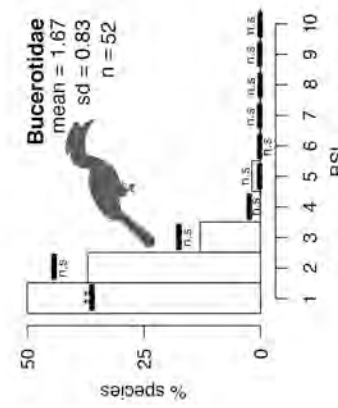
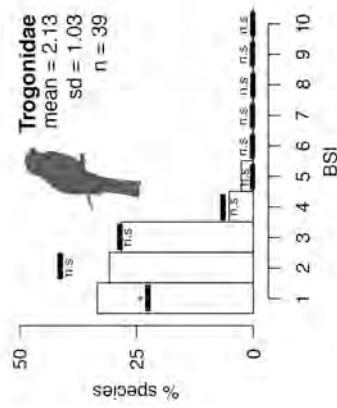
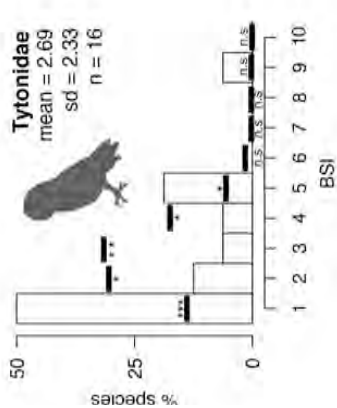
Biome	Accipitridae			Monte Carlo Analysis			
	sp	sp	(BSI=1)	Mean %	S.d.	Range	p
I	136	39	28.68	4.61	1.70	0 - 11	<0.001
II	123	4	3.25	3.68	1.60	0 - 11.4	0.959
III	93	2	2.15	2.53	1.60	0 - 9.68	0.729
IV	30	0	0.00	1.47	2.20	0 - 16.7	0.563
V	32	1	3.13	1.55	2.20	0 - 15.6	0.093
VI	86	3	3.49	2.34	1.60	0 - 9.3	0.155
VII	17	0	0.00	1.41	2.90	0 - 23.5	0.274
VIII	25	3	12.00	1.46	2.40	0 - 16	<0.001
IX	18	0	0.00	1.40	2.80	0 - 22.2	0.290
IX	4	0	0.00	1.34	5.70	0 - 50	0.056

BSI	%	Monte Carlo Analysis			
		Mean %	S.d.	Range	p
1	42.20	24.00	2.5	14 - 34	<0.001
2	26.50	35.00	3.5	22 - 51	0.00573
3	13.00	26.00	3.2	14 - 39	<0.001
4	11.40	11.00	2.1	3.4 - 19	0.899
5	3.78	2.90	1.2	0 - 7.6	0.287
6	1.62	0.44	0.49	0 - 2.9	0.038
7	1.08	0.04	0.15	0 - 1.7	0.002
8	0.00	0.002	0.03	0 - 0.61	0.997
9	0.54	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Strigidae			Monte Carlo Analysis			
	sp	sp	(BSI=1)	Mean %	S.d.	Range	p
I	95	41	43.16	12.70	3.10	3.16 - 25.3	<0.001
II	93	18	19.35	12.50	3.10	2.15 - 25.8	0.0109
III	38	2	5.263	7.82	4.20	0 - 26.3	0.225
IV	17	1	5.882	6.87	6.00	0 - 35.3	0.493
V	16	0	0.00	6.88	6.30	0 - 43.8	<0.001
VI	72	14	19.44	10.10	3.30	0 - 25	0.0031
VII	31	0	0.00	7.54	4.60	0 - 29	<0.001
VIII	14	0	0.00	6.59	6.70	0 - 50	<0.001
IX	31	2	6.452	7.44	4.60	0 - 25.8	0.714
IX	1	0	0.00	6.32	24.00	0 - 100	0.0675

Figure 2-figure supplement 2J. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Laridae, Accipitridae and Strigidae.

2. Biomic specialization



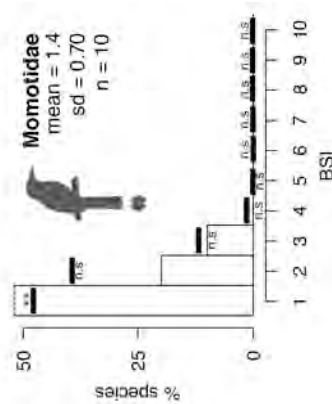
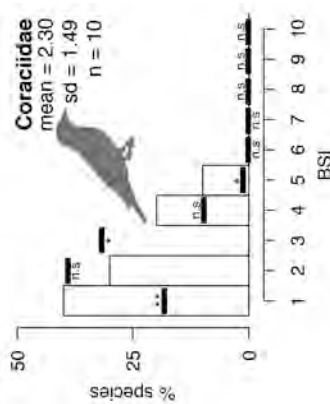
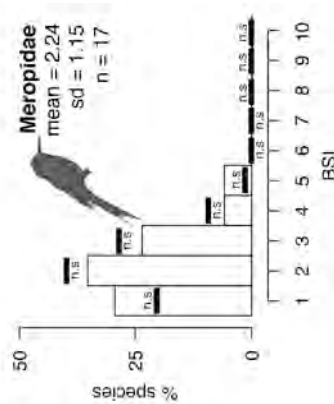
BSI	%	Monte Carlo Analysis				Tytonidae		Monte Carlo Analysis			
		Mean %	S.d.	Range	p	sp	sp (BSI=1)	Mean %	S.d.	Range	p
1	50.00	14.00	7.20	0 - 44	<0.001	12	6	8.92	7.30	0 - 41.7	<0.001
2	12.50	30.00	11.00	0 - 69	0.024	9	1	4.93	6.70	0 - 33.3	0.056
3	6.25	31.00	12.00	0 - 80	0.003	3	0	2.74	9.40	0 - 66.7	0.088
4	6.25	18.00	8.50	0 - 50	0.030	1	0	2.15	15.00	0 - 100	0.022
5	18.80	5.70	5.30	0 - 29	0.016	2	0	2.46	11.00	0 - 100	0.051
6	0.00	1.10	2.60	0 - 14	0.837	7	1	14.29	3.89	7.00	0 - 57.1
7	0.00	0.12	0.89	0 - 13	0.981	3	0	2.58	9.00	0 - 66.7	0.083
8	0.00	0.01	0.20	0 - 6.7	0.999	3	0	2.66	9.20	0 - 66.7	0.085
9	6.25	0.00	0.00	0 - 0	1.000	3	0	2.79	9.50	0 - 66.7	0.089
10	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Trogonidae		Monte Carlo Analysis			
		Mean %	S.d.	Range	p	sp	sp (BSI=1)	Mean %	S.d.	Range	p
1	33.30	23.00	5.00	5.4 - 44	0.010	30	10	15.70	5.10	0 - 36.7	<0.001
2	30.80	41.00	7.80	11 - 68	0.086	20	2	7.48	5.00	0 - 30	0.195
3	28.20	29.00	6.20	7.7 - 53	0.729	3	0	3.89	8.90	0 - 100	0.126
4	5.13	6.6	3.40	0 - 26	0.291	0	0	0.00	0.00	0 - 0	1.000
5	2.56	0.36	0.95	0 - 5.7	0.124	0	0	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000	22	1	8.22	4.80	0 - 31.8	0.128
7	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000	8	0	4.60	7.20	0 - 50	0.470
10	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Bucerotidae		Monte Carlo Analysis			
		Mean %	S.d.	Range	p	sp	sp (BSI=1)	Mean %	S.d.	Range	p
1	50.00	37.00	5.20	19 - 54	0.004	33	18	24.30	5.70	6.06 - 45.5	<0.001
2	36.50	44.00	7.00	13 - 67	0.162	32	7	21.88	5.70	6.25 - 46.9	0.872
3	11.50	16.00	4.50	2 - 32	0.169	10	1	10.00	9.60	0 - 50	0.458
4	0.00	2.20	2.00	0 - 11	0.319	2	0	8.99	20.00	0 - 100	0.210
5	1.92	0.12	0.50	0 - 4.5	0.060	0	0	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.078	0 - 2.2	0.999	8	0	10.70	11.00	0 - 62.5	<0.001
7	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	1	0	9.04	29.00	0 - 100	0.0994
9	0.00	0.00	0.00	0 - 0	1.000	1	0	9.60	29.00	0 - 100	0.106
10	0.00	0.00	0.00	0 - 0	1.000	0	0	0.00	0.00	0 - 0	1.000

Figure 2-figure supplement 2K. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Tytonidae, Trogonidae and Bucerotidae.

2. Biomic specialization



BSI	%	Monte Carlo Analysis				Meropidae				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	29.4	21.00	7.70	0-47	0.087	I	11	3	27.27	9.25	7.50	0-36.4	0.003
2	35.3	40.00	12.00	0-82	0.410	II	13	2	15.38	13.80	7.90	0-38.5	0.305
3	23.5	29.00	10.00	0-77	0.314	III/IV	5	0	0.00	4.48	8.90	0-60	0.270
4	5.88	9.40	6.10	0-36	0.170	III	3	0	0.00	3.98	11.00	0-66.7	0.133
5	5.88	1.50	2.80	0-20	0.146	IV	0	0	0.00	0.00	0.00	0-0	1.000
6	0.00	0.089	0.74	0-7.1	0.986	V	4	0	0.00	4.33	10.00	0-75	0.198
7	0.00	0.003	0.12	0-6.7	1.000	VI	0	0	0.00	0.00	0.00	0-0	1.000
8	0.00	0.00	0.00	0-0	1.000	VII	1	0	0.00	3.29	18.00	0-100	0.034
9	0.00	0.00	0.00	0-0	1.000	VIII	1	0	0.00	3.50	18.00	0-100	0.036
10	0.00	0.00	0.00	0-0	1.000	IX	0	0	0.00	0.00	0.00	0-0	1.000

BSI	%	Monte Carlo Analysis				Coraciidae				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	40.00	18.00	9.60	0-50	0.001	I	6	2	33.33	7.92	10.00	0-50	0.002
2	30.00	39.00	15.00	0-90	0.240	II	9	3	33.33	15.50	10.00	0-55.6	0.011
3	0.00	32.00	13.00	0-78	0.015	III/IV	5	0	0.00	6.69	11.00	0-60	0.443
4	20.00	9.80	8.00	0-44	0.102	III	1	0	0.00	4.26	20.00	0-100	0.045
5	10.00	1.20	3.40	0-25	0.046	IV	1	0	0.00	4.37	20.00	0-100	0.046
6	0.00	0.05	0.73	0-12	0.995	V	2	0	0.00	4.68	15.00	0-100	0.101
7	0.00	0.00	0.00	0-0	1.000	VI	2	0	0.00	4.79	15.00	0-100	0.105
8	0.00	0.00	0.00	0-0	1.000	VII	1	0	0.00	4.20	20.00	0-100	0.044
9	0.00	0.00	0.00	0-0	1.000	VIII	0	0	0.00	0.00	0.00	0-0	1.000
10	0	0.00	0.00	0-0	1.000	IX	0	0	0.00	0.00	0.00	0-0	1.000

BSI	%	Monte Carlo Analysis				Momotidae				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Biome	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
1	70.00	48.00	14.00	0-80	0.007	I	6	4	66.67	38.80	15.00	0-100	0.006
2	20.00	39.00	16.00	0-100	0.099	II	4	2	50.00	26.00	19.00	0-100	0.030
3	10.00	12.00	10.00	0-67	0.417	III/IV	1	0	0.00	17.30	38.00	0-100	0.209
4	0.00	1.50	4.20	0-29	0.882	III	0	0	0.00	0.00	0.00	0-0	1.000
5	0.00	0.08	1.00	0-17	0.994	IV	0	0	0.00	0.00	0.00	0-0	1.000
6	0.00	0.00	0.00	0-0	1.000	V	2	1	50.00	19.50	27.00	0-100	0.029
7	0.00	0.00	0.00	0-0	1.000	VI	0	0	0.00	0.00	0.00	0-0	1.000
8	0.00	0.00	0.00	0-0	1.000	VII	0	0	0.00	0.00	0.00	0-0	1.000
9	0.00	0.00	0.00	0-0	1.000	VIII	1	0	0.00	17.10	38.00	0-100	0.206
10	0.00	0.00	0.00	0-0	1.000	IX	0	0	0.00	0.00	0.00	0-0	1.000

Figure 2-figure supplement 2L. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Meropidae, Coraciidae and Momotidae.

2. Biomic specialization

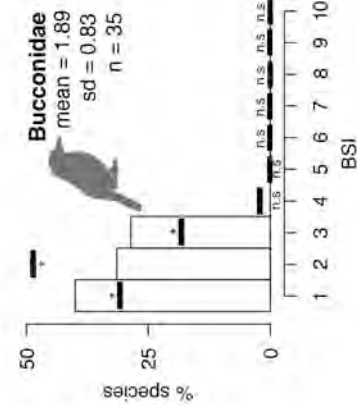
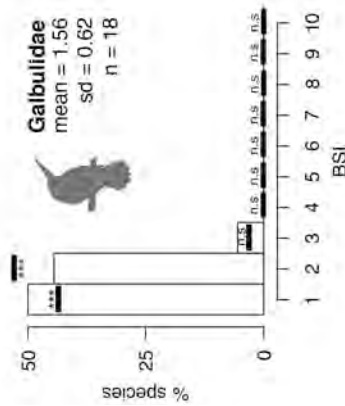
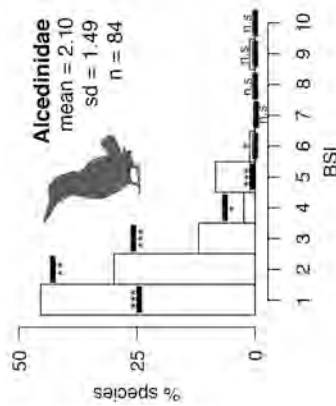


Figure 2-figure supplement 2M. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds). in this plate: Alcedinidae, Galbulidae and Bucconidae.

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	45.20	24.00	3.4	9.1 - 37	<0.001	19.60	3.50	5.71-31.4	<0.001
2	29.80	43.00	5.3	24 - 64	0.006	7.82	3.20	0 - 20.4	0.168
3	11.90	25.00	4.2	8.4 - 45	<0.001	4.38	4.20	0 - 23.8	<0.001
4	2.38	6.50	2.3	0 - 16	0.0132	3.20	10.00	0 - 66.7	0.103
5	8.33	0.78	0.94	0 - 5.1	<0.001	3.72	7.70	0 - 50	0.258
6	1.19	0.04	0.23	0 - 2.5	0.036	4.30	4.40	0 - 30	0.046
7	0.00	0.001	0.039	0 - 1.3	0.999	3.57	9.20	0 - 75	0.157
8	0.00	0.00	0.00	0 - 0	1.000	3.35	13.00	0 - 100	0.071
9	1.19	0.00	0.00	0 - 0	1.000	3.13	17.00	0 - 100	0.032
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	50.00	44.00	5.00	35 - 50	<0.001	41.90	4.00	35.3 - 47.1	<0.001
2	44.40	54.00	6.80	44 - 65	<0.001	5.21	5.00	0 - 10	<0.001
3	5.56	3.00	2.90	0 - 5.9	0.325	2.50	16.00	0 - 100	0.026
4	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
5	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	40.00	31.00	4.90	12 - 49	0.014	29.20	4.80	12.1 - 45.5	0.005
2	31.40	49.00	8.20	17 - 82	0.011	3.66	3.50	0 - 10.5	0.133
3	28.60	19.00	4.90	0 - 36	0.019	1.83	6.70	0 - 50	0.078
4	0.00	2.00	2.20	0 - 12	0.459	0.00	0.00	0 - 0	1.000
5	0.00	0.04	0.35	0 - 3	0.985	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000	2.24	4.70	0 - 22.2	0.239
7	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000	1.63	13.00	0 - 100	0.017
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000

2. Biomic specialization

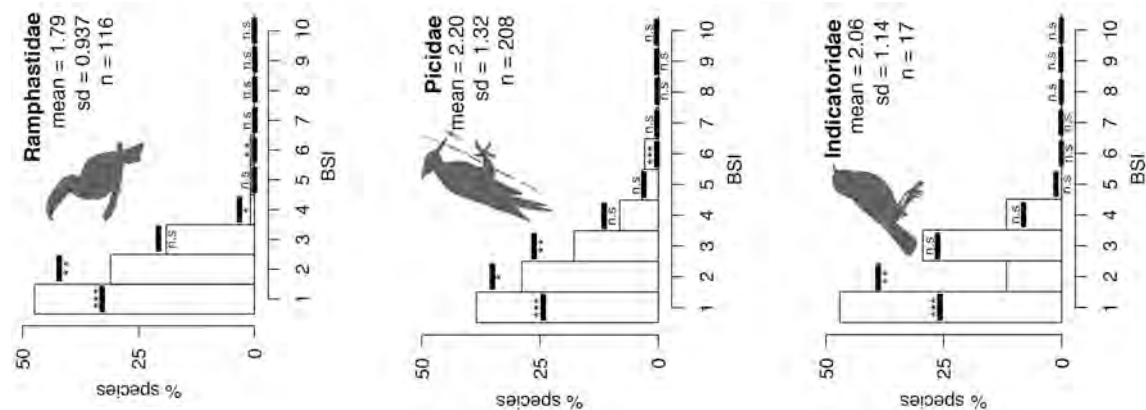
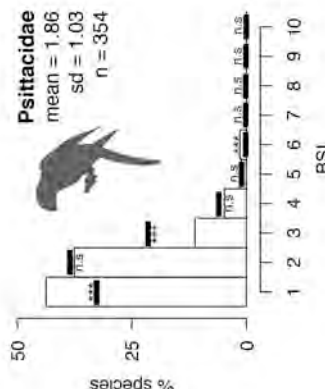
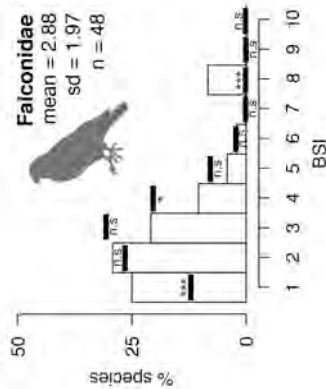


Figure 2-figure supplement 2N. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds), in this plate: Ramphastidae, Picidae and Indicatoridae.

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	47.40	33.00	3.40	22 - 45	<0.001	20.1	3.9	5.8 - 34.8	<0.001
2	31.00	42.00	4.70	25 - 58	0.008	18.9	4	4.55 - 33.3	0.012
3	19.00	21.00	3.30	10 - 33	0.390	9.06	8.2	0 - 50	0.431
4	0.86	3.40	1.60	0 - 11	0.015	8.46	20	0 - 100	0.194
5	0.86	0.21	0.44	0 - 2.9	0.261	8.92	29	0 - 100	0.098
6	0.86	0.01	0.08	0 - 0.98	0.007	14.1	4.4	0 - 32.7	0.133
7	0.00	0.00	0.00	0 - 0	1.000	9.04	29	0 - 100	0.099
8	0.00	0.00	0.00	0 - 0	1.000	7.93	19	0 - 100	0.178
9	0.00	0.00	0.00	0 - 0	1.000	8.71	11	0 - 66.7	0.001
10	0.00	0.00	0.00	0 - 0	1.000	0	0	0 - 0	1.000

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	38.5	24.00	2.40	14 - 36	<0.001	13.60	2.80	3.51-25.4	<0.001
2	28.8	35.00	3.30	21 - 48	0.026	12.00	2.90	1.98-23.8	0.074
3	17.8	25.00	3.00	15 - 37	0.002	7.71	4.00	0 - 25.6	0.114
4	8.17	11.00	2.00	4.1 - 19	0.079	6.56	7.10	0 - 41.7	0.005
5	3.37	2.70	1.10	0 - 7.5	0.389	6.61	6.90	0 - 38.5	0.272
6	2.88	0.41	0.44	0 - 2.6	<0.001	9.99	3.10	0 - 22.5	0.684
7	0.48	0.04	0.13	0 - 1.6	0.069	7.08	4.90	0 - 29.6	0.155
8	0.00	0.00	0.03	0 - 0.53	0.997	7.20	4.60	0 - 30.0	0.578
9	0.00	0.00	0.005	0 - 0.52	1.000	7.50	4.30	0 - 27.8	0.391
10	0.00	0.00	0.00	0 - 0	1.000	6.12	24.00	0 - 100	0.065

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	47.10	26.00	8.50	0 - 53	0.002	13.00	10.00	0 - 55.6	<0.001
2	11.80	39.00	12.00	0 - 82	0.005	14.90	9.80	0 - 60	0.172
3	29.40	26.00	9.90	0 - 64	0.528	8.08	13.00	0 - 75	0.415
4	11.80	8.10	6.00	0 - 43	0.464	0.00	0.00	0 - 0	1.000
5	0.00	1.10	2.60	0 - 20	0.828	6.58	17.00	0 - 100	0.147
6	0.00	0.08	0.70	0 - 7.7	0.988	11.60	10.00	0 - 50	0.292
7	0.00	0.00	0.07	0 - 7.1	1.000	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000	6.99	25.00	0 - 100	0.075
9	0.00	0.00	0.00	0 - 0	1.000	6.16	24.00	0 - 100	0.066
10	0.00	0.00	0.00	0 - 0	1.000	0.00	0.00	0 - 0	1.000



BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	25.00	12.00	3.90	0 - 28	<0.001	2.84	3.20	0 - 19.2	<0.001
2	29.20	27.00	5.80	4.3 - 51	0.453	4.09	3.10	0 - 18.9	0.227
3	20.80	30.00	6.80	8.3 - 57	0.0691	2.98	3.10	0 - 17.9	0.251
4	10.40	20.00	5.30	2.2 - 45	0.0173	2.38	3.40	0 - 21.1	0.007
5	4.17	8.20	3.50	0 - 22	0.0735	2.21	3.80	0 - 40	0.042
6	2.08	2.10	2.00	0 - 11	0.505	2.51	3.30	0 - 19	0.723
7	0.00	0.33	0.83	0 - 8.3	0.853	2.23	3.50	0 - 17.6	0.481
8	8.33	0.03	0.86	0 - 2.3	<0.001	2.29	3.60	0 - 23.5	0.006
9	0.00	0.00	0.06	0 - 2.2	0.999	2.03	3.80	0 - 28.6	0.332
10	0.00	0.00	0.00	0 - 0	1.000	1.79	5.40	0 - 33.3	0.004

BSI	%	Monte Carlo Analysis				Monte Carlo Analysis			
		Mean %	S.d.	Range	p	Mean %	S.d.	Range	p
1	43.80	33.00	2.00	23 - 40	<0.001	21.70	2.40	12.6 - 31.1	<0.001
2	37.60	39.00	2.70	29 - 50	0.540	17.30	2.50	8.33 - 26.2	0.386
3	11.30	21.00	2.10	14 - 30	<0.001	10.70	4.10	0 - 27.8	0.420
4	4.80	6.20	1.20	2.4 - 11	0.123	16.67	6.80	0 - 44.4	0.093
5	1.13	1.10	0.55	0 - 3.7	0.787	10.00	5.10	0 - 32.4	<0.001
6	1.41	0.10	0.18	0 - 1.2	<0.001	12.70	3.20	1.98 - 25.7	0.092
7	0.00	0.01	0.04	0 - 0.32	0.983	9.92	5.40	0 - 37.9	0.061
8	0.00	0.00	0.01	0 - 0.31	1.000	9.28	9.60	0 - 55.6	<0.001
9	0.00	0.00	0.00	0 - 0	1.000	10.20	4.90	0 - 36.1	0.370
10	0.00	0.00	0.00	0 - 0	1.000	9.12	14.00	0 - 100	0.464

Figure 2-figure supplement 2O. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species (excluding migratory birds), in this plate: Falconidae and Psittacidae.

2. Biomic specialization

Appendix 2.8.5. Supplementary data of Figure 2 (Fig. S3 from A to F) – Migratory species (fam > 10 spp)

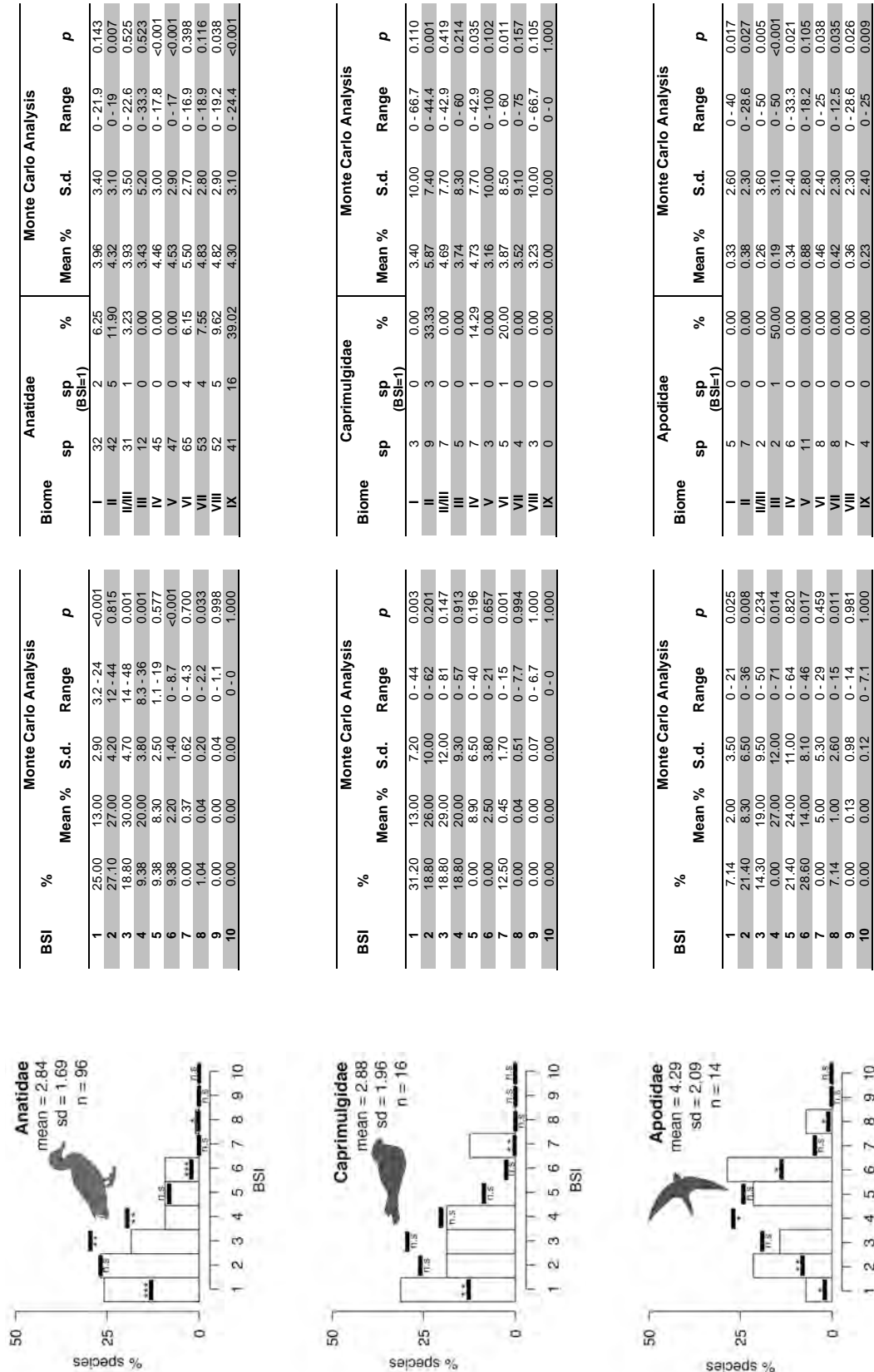
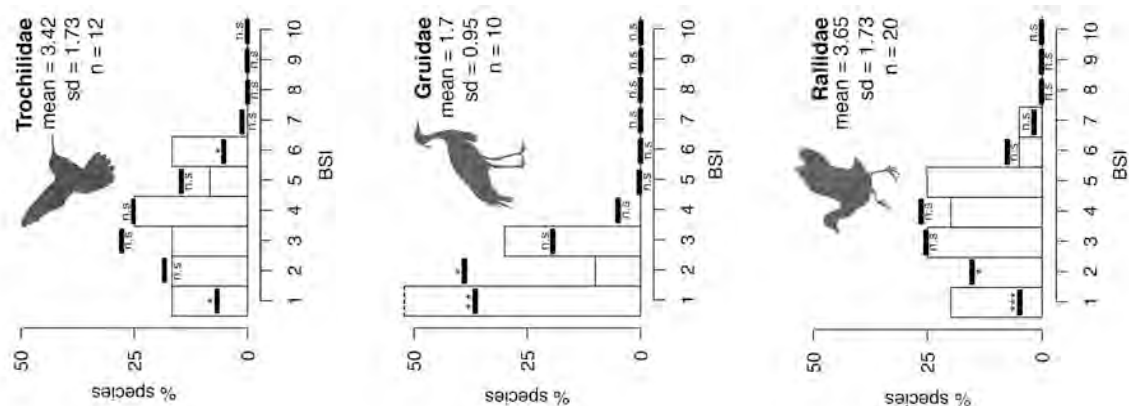


Figure 2-figure supplement 3A. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species considering only migratory species. in this plate: Anatidae, Caprimulgidae and Apodidae.

2. Biomic specialization



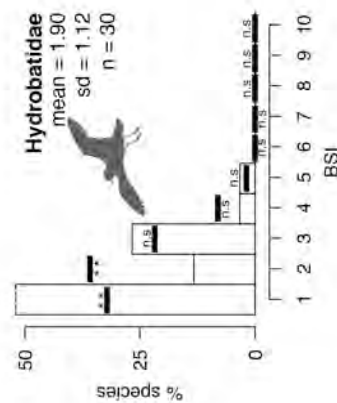
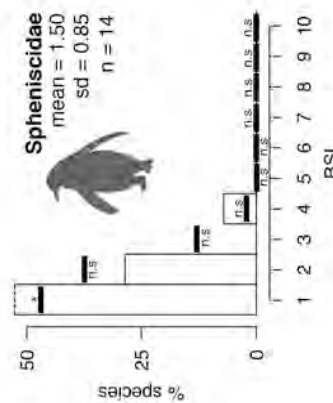
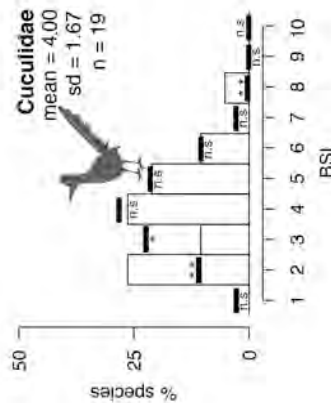
Trochilidae					Monte Carlo Analysis				
Biome	sp	sp (BSI=1)	%		Mean %	S.d.	Range		p
I	1	0	0.00		0.94	9.70	0 - 100		0.009
II	2	0	0.00		1.15	7.50	0 - 50		0.023
III/III	5	1	20.00		1.77	5.80	0 - 40		0.001
IV	4	1	25.00		1.52	6.00	0 - 50		0.001
V	6	0	0.00		1.93	5.50	0 - 33.3		0.128
VI	4	0	0.00		1.62	6.30	0 - 50		0.068
VII	8	0	0.00		2.97	5.80	0 - 37.5		0.285
VIII	6	0	0.00		1.96	5.60	0 - 33.3		0.129
IX	4	0	0.00		1.56	6.20	0 - 75		0.066
	1	0	0.00		1.08	10.00	0 - 100		0.011

Gruidae					Monte Carlo Analysis				
Biome	sp	sp (BSI=1)	%		Mean %	S.d.	Range		p
I	0	0	0.00		0.00	0.00	0 - 0		1.000
II	1	0	0.00		13.40	34.00	0 - 100		0.155
III/III	1	0	0.00		12.90	34.00	0 - 100		0.149
IV	0	0	0.00		0.00	0.00	0 - 0		1.000
V	0	0	0.00		0.00	0.00	0 - 0		1.000
VI	4	1	25.00		19.20	18.00	0 - 75		0.173
VII	5	3	60.00		23.40	17.00	0 - 80		0.003
VIII	4	1	25.00		19.40	18.00	0 - 100		0.181
IX	2	1	50.00		14.70	25.00	0 - 100		0.018

Rallidae					Monte Carlo Analysis				
Biome	sp	sp (BSI=1)	%		Mean %	S.d.	Range		p
I	7	0	0.00		1.11	3.90	0 - 42.9		0.083
II	11	1	9.09		1.57	3.70	0 - 36.4		0.012
III/III	7	0	0.00		1.11	4.00	0 - 42.9		0.082
IV	2	0	0.00		0.82	6.30	0 - 50		0.017
V	9	0	0.00		1.34	3.70	0 - 22.2		0.133
VI	7	0	0.00		1.17	4.00	0 - 42.9		0.087
VII	13	2	15.38		2.11	3.80	0 - 23.1		0.001
VIII	9	0	0.00		1.31	3.80	0 - 33.3		0.128
IX	7	1	14.29		1.14	4.00	0 - 28.6		0.001
	1	0	0.00		0.85	9.20	0 - 100		0.009

Figure 2-figure supplement 3B. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species considering only migratory species. in this plate: Trochilidae, Gruidae and Rallidae.

2. Biomic specialization



BSI	Monte Carlo Analysis			
	%	Mean %	S.d.	p
1	0.00	2.90	3.60	0.21
2	26.30	11.00	6.10	0.003
3	10.50	23.00	8.90	0.042
4	26.30	28.00	10.00	0.68
5	21.10	22.00	8.90	0.58
6	10.50	11.00	6.20	0.37
7	0.00	3.00	3.70	0.22
8	5.26	0.47	1.50	0.11
9	0.00	0.02	0.36	0.56
10	0.00	0.00	0.09	0.53

BSI	Monte Carlo Analysis			
	%	Mean %	S.d.	p
1	64.30	47.00	10.00	9.1 - 79
2	28.60	37.00	14.00	0.91
3	0.00	13.00	8.30	0.45
4	7.14	2.40	4.10	0.30
5	0.00	0.24	1.40	0.10
6	0.00	0.01	0.32	0.10
7	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00

BSI	Monte Carlo Analysis			
	%	Mean %	S.d.	p
1	53.30	32.00	7.10	7.7 - 60
2	13.30	36.00	9.30	4 - 69
3	26.70	22.00	7.50	0 - 54
4	3.33	8.20	4.80	0 - 39
5	3.33	2.00	2.60	0 - 16
6	0.00	0.30	1.00	0 - 8.3
7	0.00	0.04	0.37	0 - 4.3
8	0.00	0.00	0.09	0 - 4
9	0.00	0.00	0.00	0 - 0
10	0.00	0.00	0.00	0 - 0

Biome	Cuculidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	10	0	0.00	0.67	2.60	0 - 30	0.070
II	14	0	0.00	1.16	2.80	0 - 14.3	0.184
III/III	7	0	0.00	0.46	2.50	0 - 28.6	0.033
III	1	0	0.00	0.30	5.50	0 - 100	0.003
IV	5	0	0.00	0.41	2.80	0 - 20	0.021
V	12	0	0.00	0.84	2.60	0 - 16.7	0.109
VI	11	0	0.00	0.72	2.50	0 - 18.2	0.085
VII	7	0	0.00	0.51	2.70	0 - 28.6	0.037
VIII	7	0	0.00	0.48	2.60	0 - 28.6	0.035
IX	2	0	0.00	0.32	4.00	0 - 50	0.006

Biome	Spheniscidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	0	0	0.00	0.00	0.00	0 - 0	1.000
II	0	0	0.00	0.00	0.00	0 - 0	1.000
III/III	0	0	0.00	0.00	0.00	0 - 0	1.000
III	2	0	0.00	13.90	24.00	0 - 100	0.356
IV	2	0	0.00	14.10	24.00	0 - 100	0.363
V	2	0	0.00	13.90	24.00	0 - 100	0.356
VI	2	0	0.00	13.90	24.00	0 - 100	0.358
VII	3	1	33.33	15.30	20.00	0 - 100	0.052
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	10	8	80.00	42.60	11.00	0 - 80	<0.001

Biome	Hydrobatidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	4	1	25.00	12.60	16.00	0 - 100	0.085
II	3	0	0.00	12.10	19.00	0 - 100	0.476
III/III	2	0	0.00	11.40	22.00	0 - 100	0.279
III	6	3	50.00	13.60	14.00	0 - 83.3	0.003
IV	5	0	0.00	12.80	15.00	0 - 80	<0.001
V	7	1	14.29	14.00	13.00	0 - 71.4	0.336
VI	11	2	18.18	17.00	10.00	0 - 72.7	0.381
VII	3	1	33.33	12.10	19.00	0 - 100	0.041
VIII	3	0	0.00	12.10	19.00	0 - 100	0.477
IX	13	8	61.54	19.10	9.80	0 - 53.8	<0.001

Figure 2-figure supplement 3C. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species considering only migratory species. in this plate: Cuculidae, Spheniscidae and Hydrobatidae.

2. Biomic specialization

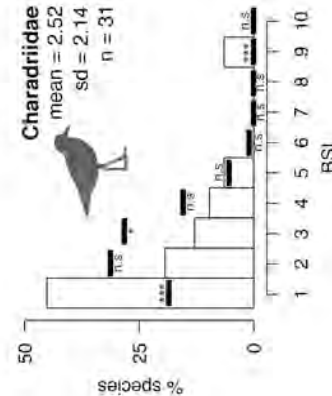
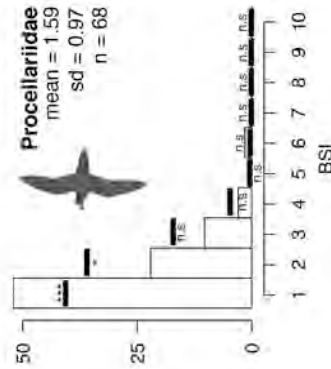
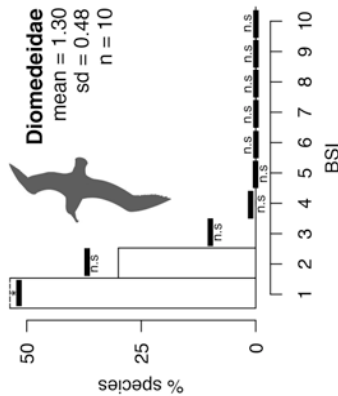


Figure 2-figure supplement 3D. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species considering only migratory species. in this plate: Diomedelidae, Procellariidae and Charadriidae.

BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	70.00	52.00	14.00	0 - 90	0.037
2	30.00	37.00	16.00	0 - 86	0.570
3	0.00	10.00	9.70	0 - 50	0.372
4	0.00	1.20	3.80	0 - 33	0.913
5	0.00	0.05	0.80	0 - 17	0.997
6	0.00	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	63.20	41.00	5.10	22 - 59	<0.001
2	22.10	36.00	6.40	14 - 63	0.012
3	10.30	17.00	4.50	3.2 - 35	0.061
4	2.94	4.90	2.60	0 - 18	0.241
5	0.00	0.86	1.20	0 - 7.7	0.602
6	1.47	0.09	0.40	0 - 3.9	0.054
7	0.00	0.00	0.00	0 - 1.9	0.997
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.02	0 - 1.9	1.000
10	0.00	0.00	0.00	0 - 0	1.000

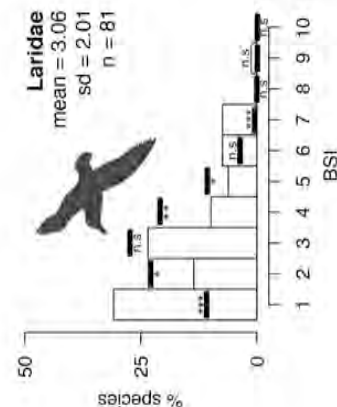
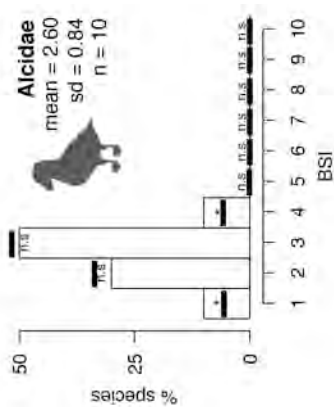
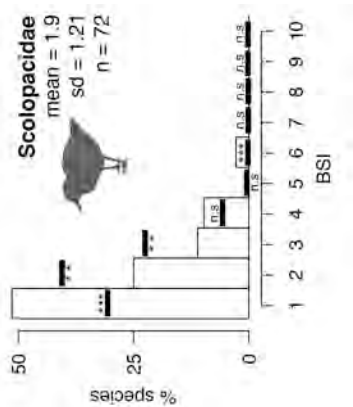
BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	45.20	18.00	5.70	0 - 37	<0.001
2	19.40	31.00	8.00	3.4 - 61	0.061
3	12.90	29.00	8.10	3.2 - 61	0.015
4	9.68	15.00	5.90	0 - 38	0.125
5	6.45	5.30	3.70	0 - 23	0.739
6	0.00	1.20	1.90	0 - 13	0.691
7	0.00	0.16	0.73	0 - 6.9	0.953
8	0.00	0.02	0.23	0 - 6.5	0.996
9	6.45	0.00	0.09	0 - 3.6	<0.001
10	0.00	0.00	0.00	0 - 0	1.000

Biome	Diomedelidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	0	0	0.00	0.00	0.00	0 - 0	1.000
II	1	0	0.00	20.70	41.00	0 - 100	0.261
III/II	0	0	0.00	0.00	0.00	0 - 0	1.000
III	1	0	0.00	20.00	40.00	0 - 100	0.250
IV	0	0	0.00	0.00	0.00	0 - 0	1.000
V	3	3	100.00	25.40	24.00	0 - 100	<0.001
VI	0	0	0.00	0.00	0.00	0 - 0	1.000
VII	2	0	0.00	22.70	29.00	0 - 100	0.708
VIII	0	0	0.00	0.00	0.00	0 - 0	1.000
IX	6	4	66.67	45.20	16.00	0 - 100	0.026

Biome	Procellariidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	12	7	58.33	19.30	11.00	0 - 66.7	<0.001
II	4	2	50.00	16.70	18.00	0 - 100	0.013
III/II	3	2	66.67	16.40	21.00	0 - 100	0.004
III	3	2	66.67	16.40	21.00	0 - 100	0.005
IV	10	3	30.00	18.90	12.00	0 - 70	0.106
V	27	11	40.74	26.40	7.60	0 - 55.6	0.018
VI	14	1	7.14	20.20	10.00	0 - 64.3	0.034
VII	9	2	22.22	18.20	13.00	0 - 66.7	0.266
VIII	3	0	0.00	16.50	21.00	0 - 100	0.727
IX	23	13	56.52	24.10	8.10	0 - 56.5	<0.001

Biome	Charadriidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	3	0	0.00	4.61	12.00	0 - 100	0.152
II	5	2	40.00	4.94	9.60	0 - 60	0.001
III/II	2	0	0.00	4.54	15.00	0 - 100	0.097
III	4	0	0.00	4.64	10.00	0 - 75	0.211
IV	6	0	0.00	5.20	8.90	0 - 50	0.387
V	7	0	0.00	5.35	8.20	0 - 42.9	0.487
VI	16	2	12.50	8.51	6.40	0 - 37.5	0.153
VII	18	7	38.89	9.76	6.40	0 - 38.9	<0.001
VIII	7	0	0.00	5.32	8.30	0 - 57.1	0.477
IX	10	3	30.00	5.96	7.20	0 - 50	0.001

2. Biomic specialization



BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	51.40	30.00	4.30	13 - 48	<0.001
2	25.00	40.00	6.00	12 - 63	0.004
3	11.10	23.00	4.50	6.1 - 41	0.003
4	9.72	5.70	2.50	0 - 17	0.061
5	0.00	0.63	0.94	0 - 6.2	0.649
6	2.78	0.03	0.23	0 - 1.6	<0.001
7	0.00	0.00	0.03	0 - 1.6	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	10.00	5.50	5.80	0 - 20	0.049
2	30.00	34.00	12.00	0 - 50	0.884
3	50.00	55.00	11.00	40 - 89	0.977
4	10.00	5.70	5.00	0 - 11	0.023
5	0.00	0.00	0.00	0 - 0	1.000
6	0.00	0.00	0.00	0 - 0	1.000
7	0.00	0.00	0.00	0 - 0	1.000
8	0.00	0.00	0.00	0 - 0	1.000
9	0.00	0.00	0.00	0 - 0	1.000
10	0.00	0.00	0.00	0 - 0	1.000

BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	30.90	12.00	3.10	2.5 - 23	<0.001
2	13.60	23.00	4.30	8.8 - 40	0.010
3	23.50	28.00	5.10	12 - 45	0.247
4	9.88	21.00	4.40	6.2 - 38	0.003
5	6.17	11.00	3.20	0 - 24	0.041
6	7.41	4.00	2.00	0 - 14	0.079
7	7.41	0.97	1.10	0 - 7.6	<0.001
8	0.00	0.16	0.45	0 - 3.8	0.883
9	1.23	0.02	0.14	0 - 1.4	0.012
10	0.00	0.00	0.02	0 - 1.2	1.000

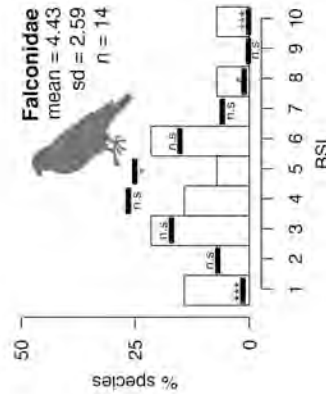
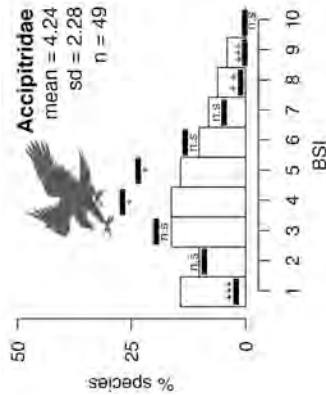
Biome	Scolopacidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	1	0	0.00	7.27	26.00	0 - 100
II	2	0	0.00	7.61	19.00	0 - 100
III/IIII	2	0	0.00	8.07	19.00	0 - 100
III	0	0	0.00	0.00	0.00	0 - 0
IV	3	0	0.00	7.79	16.00	0 - 100
V	4	0	0.00	8.02	13.00	0 - 75
VI	24	0	0.00	11.20	6.00	0 - 37.5
VII	17	0	0.00	9.72	6.80	0 - 41.2
VIII	42	12	28.57	17.90	4.90	2.38 - 38.1
IX	42	25	59.52	17.90	4.90	2.38 - 35.7

Biome	Alcidae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	0	0	0.00	0.00	0.00	0 - 0
II	0	0	0.00	0.00	0.00	0 - 0
III/IIII	0	0	0.00	0.00	0.00	0 - 0
III	0	0	0.00	0.00	0.00	0 - 0
IV	1	0	0.00	0.29	5.40	0 - 100
V	0	0	0.00	0.00	0.00	0 - 0
VI	7	0	0.00	0.89	3.50	0 - 14.3
VII	0	0	0.00	0.00	0.00	0 - 0
VIII	9	0	0.00	2.66	4.70	0 - 11.1
IX	9	1	11.11	2.72	4.80	0 - 11.1

Biome	Laridae			Monte Carlo Analysis		
	sp	sp (BSI=1)	%	Mean %	S.d.	Range
I	23	1	4.35	3.49	3.70	0 - 21.7
II	27	1	3.70	3.70	3.60	0 - 22.2
III/IIII	18	0	0.00	3.10	4.00	0 - 22.2
III	22	5	22.73	3.37	3.80	0 - 22.7
IV	24	1	4.17	3.45	3.60	0 - 20.8
V	28	1	3.57	3.81	3.50	0 - 21.4
VI	37	1	2.70	4.50	3.30	0 - 18.9
VII	30	6	20.00	3.95	3.50	0 - 20
VIII	20	1	5.00	3.32	4.00	0 - 25
IX	19	8	42.11	3.16	4.00	0 - 26.3

Figure 2-figure supplement 3E. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species considering only migratory species. in this plate: Scolopacidae, Alcidae and Laridae.

2. Biomic specialization



BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	14.30	2.10	1.90	0 - 10	<0.001
2	10.20	8.70	3.60	0 - 22	0.326
3	16.30	20.00	5.20	2 - 43	0.259
4	16.30	27.00	6.30	4.1 - 53	0.027
5	14.30	23.00	5.70	4.1 - 49	0.035
6	10.20	13.00	4.30	0 - 31	0.217
7	8.16	4.80	2.70	0 - 16	0.080
8	6.12	1.00	1.40	0 - 8.3	0.003
9	4.08	0.11	0.48	0 - 4.2	<0.001
10	0.00	0.01	0.11	0 - 2.1	0.997

BSI	Monte Carlo Analysis				
	%	Mean %	S.d.	Range	p
1	14.30	1.60	3.20	0 - 21	<0.001
2	7.14	7.00	6.10	0 - 29	0.348
3	21.40	17.00	8.90	0 - 50	0.241
4	14.30	26.00	12.00	0 - 71	0.090
5	7.14	25.00	11.00	0 - 71	0.017
6	21.40	15.00	8.50	0 - 46	0.155
7	0.00	5.90	5.70	0 - 29	0.390
8	7.14	1.30	3.00	0 - 21	0.015
9	0.00	0.14	1.00	0 - 14	0.981
10	7.14	0.01	0.23	0 - 7.7	<0.001

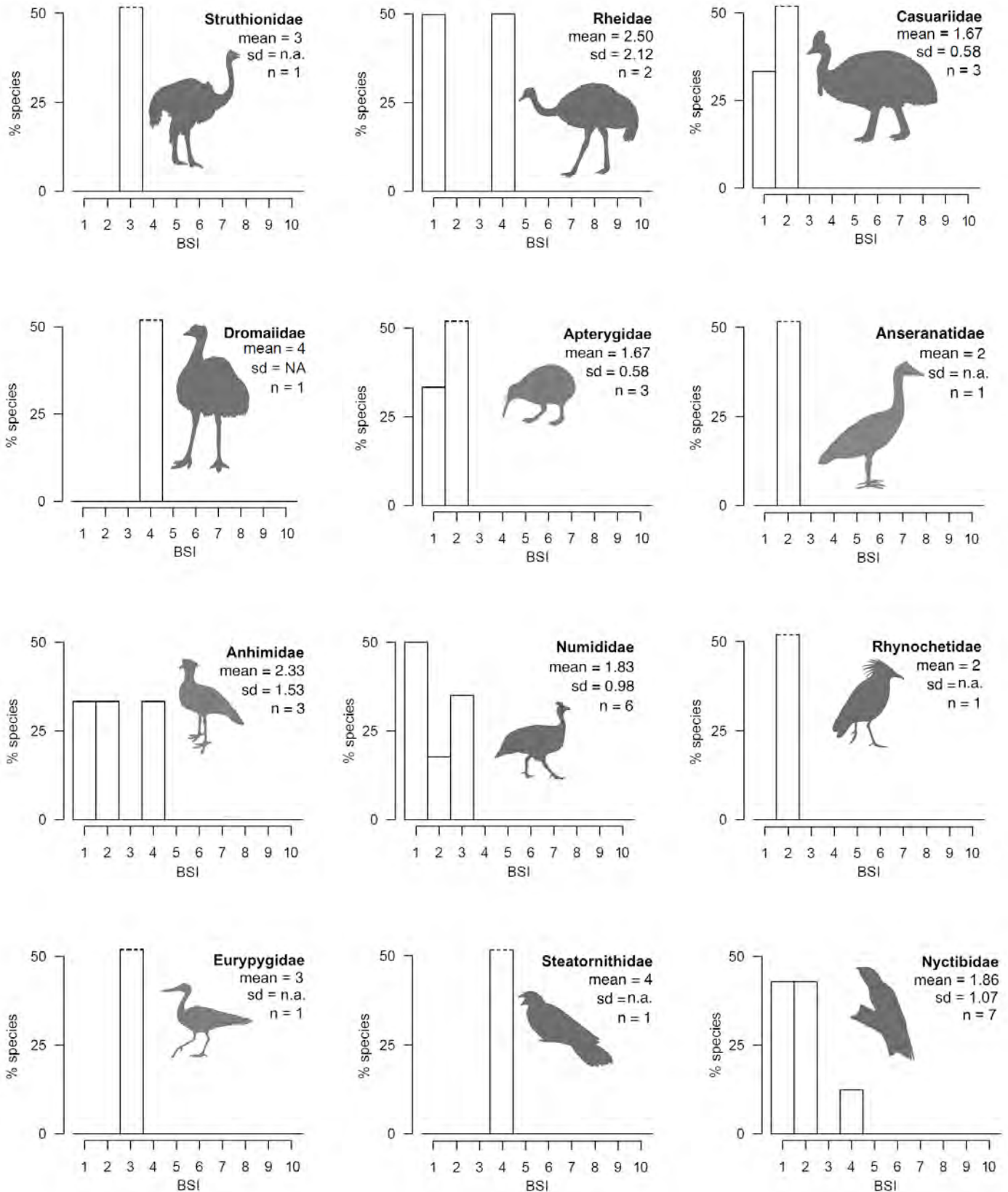
Biome	Accipitridae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	8	0	0.00	0.22	1.70	0 - 12.5	0.018
II	14	0	0.00	0.30	1.50	0 - 14.3	0.043
III	19	1	5.26	0.33	1.30	0 - 10.5	0.002
IV	17	0	0.00	0.31	1.30	0 - 11.8	0.054
V	25	0	0.00	0.44	1.30	0 - 8	0.118
VI	22	0	0.00	0.39	1.30	0 - 13.6	0.092
VII	34	0	0.00	0.71	1.40	0 - 11.8	0.281
VIII	36	4	11.11	0.83	1.50	0 - 11.1	<0.001
IX	25	1	4.00	0.44	1.30	0 - 12	0.004
	8	1	12.50	0.23	1.70	0 - 12.5	<0.001

Biome	Falconidae			Monte Carlo Analysis			
	sp	sp (BSI=1)	%	Mean %	S.d.	Range	p
I	1	0	0.00	0.12	3.50	0 - 100	0.001
II	5	0	0.00	0.23	2.20	0 - 20	0.012
III	5	0	0.00	0.24	2.20	0 - 20	0.012
IV	7	1	14.29	0.27	1.90	0 - 14.3	<0.001
V	9	1	11.11	0.44	2.20	0 - 22.2	<0.001
VI	5	0	0.00	0.23	2.10	0 - 20	0.012
VII	10	0	0.00	0.55	2.30	0 - 20	0.058
VIII	9	0	0.00	0.46	2.20	0 - 22.2	0.043
IX	8	0	0.00	0.33	2.00	0 - 25	0.027
	3	0	0.00	0.14	2.20	0 - 33.3	0.004

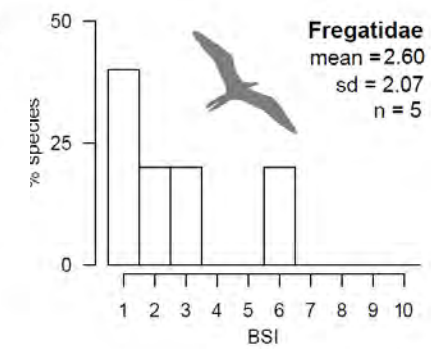
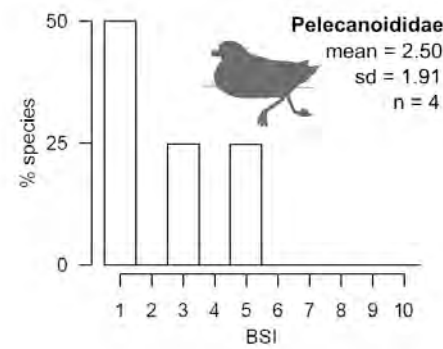
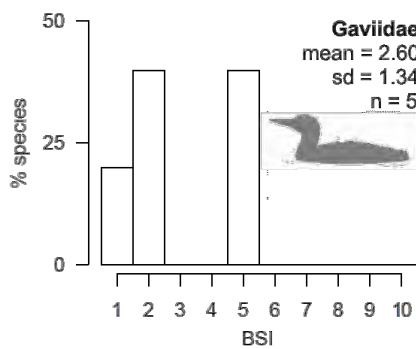
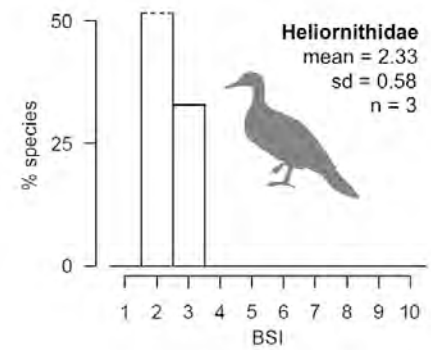
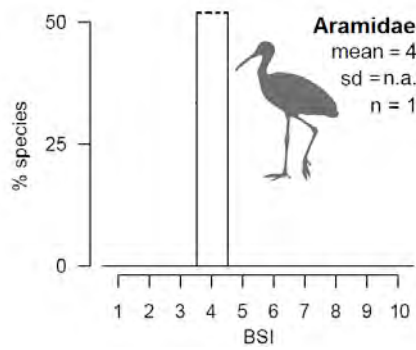
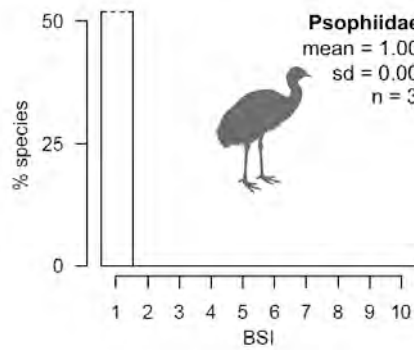
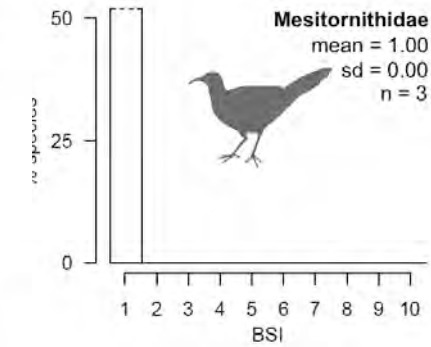
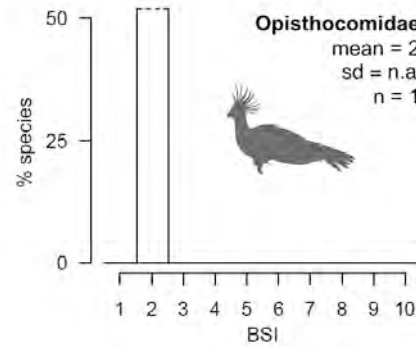
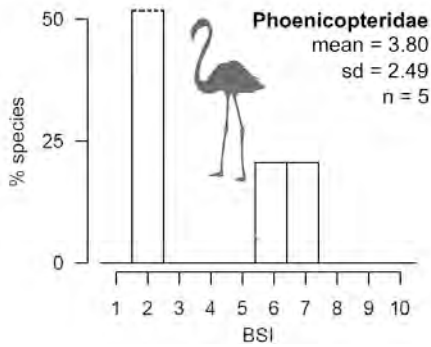
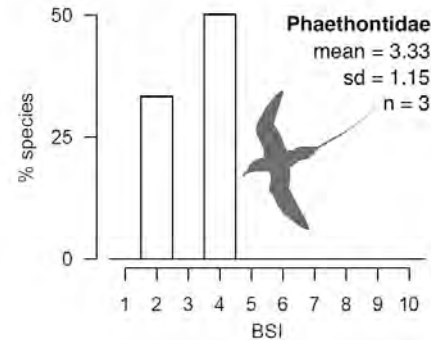
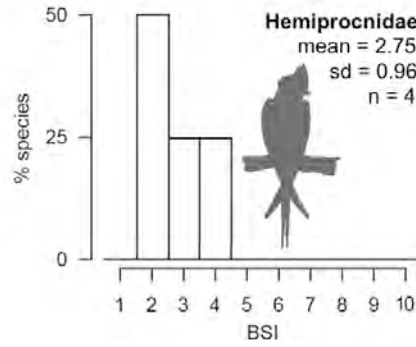
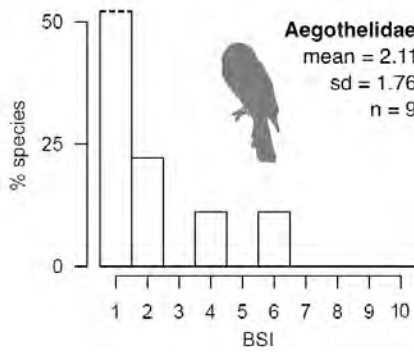
Figure 2-figure supplement 3F. Data and Results for the Monte Carlo Analysis in the Non-Passerine Families with more than 10 species considering only migratory species, in this plate: Accipitridae and Falconidae.

2. Biomic specialization

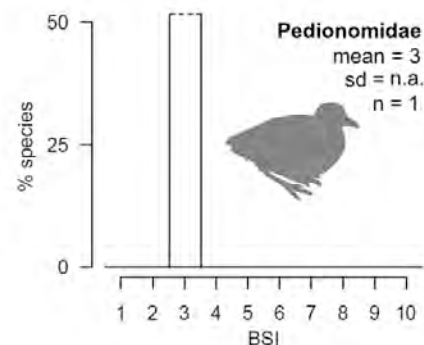
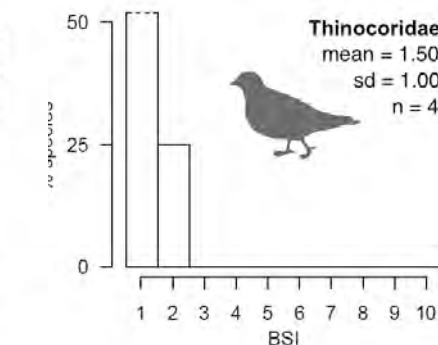
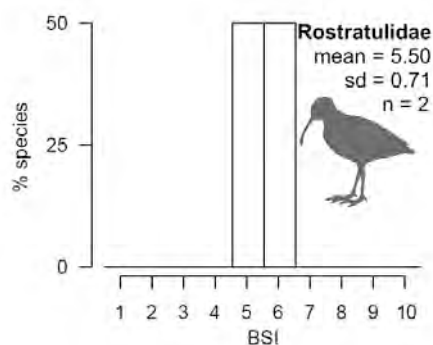
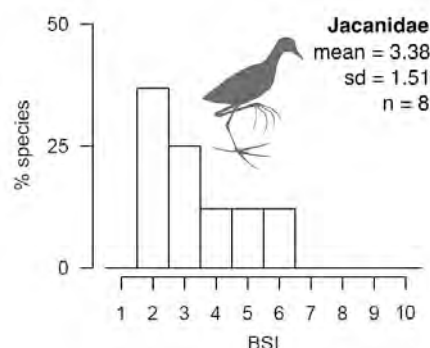
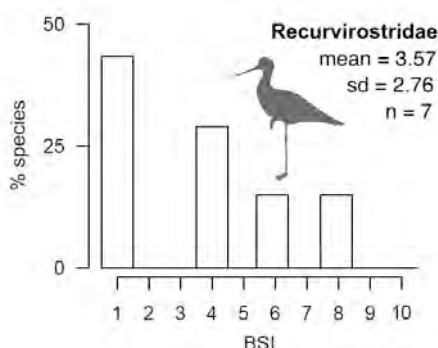
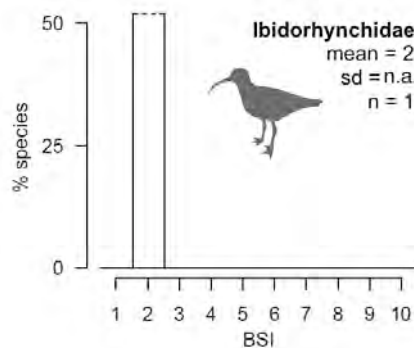
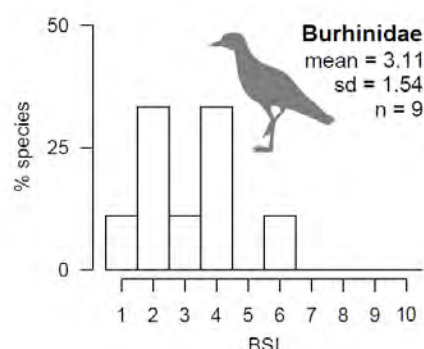
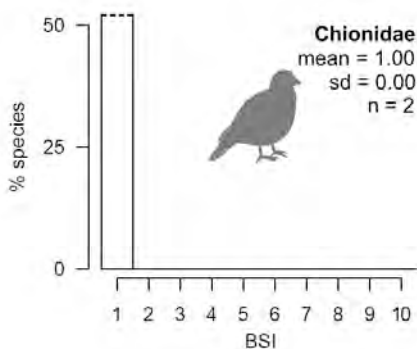
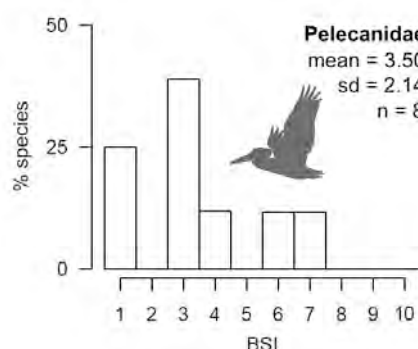
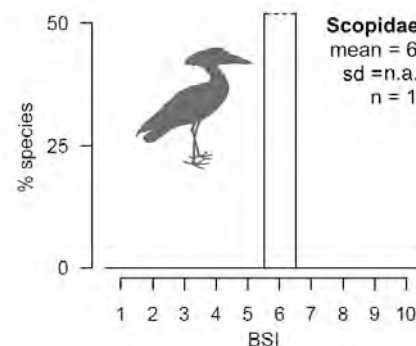
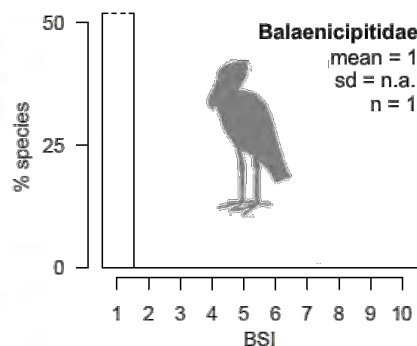
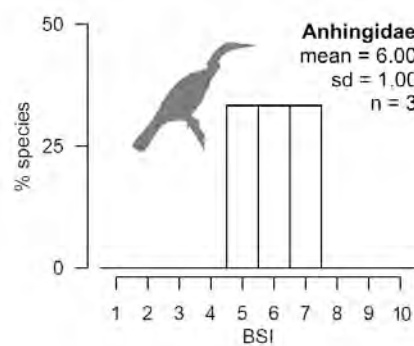
Appendix 2.8.6. Supplementary data of Figure 2 (Figures S4) – Species of families (< 10 spp)



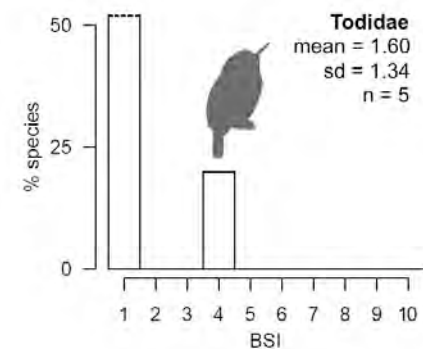
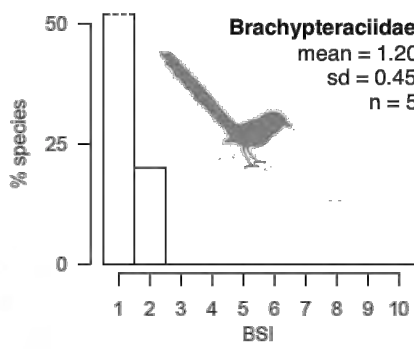
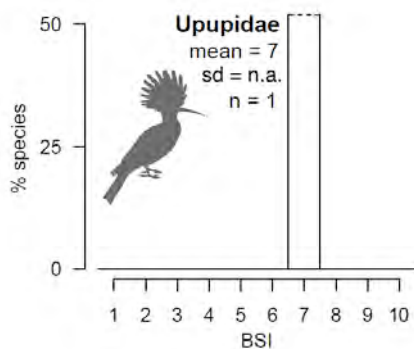
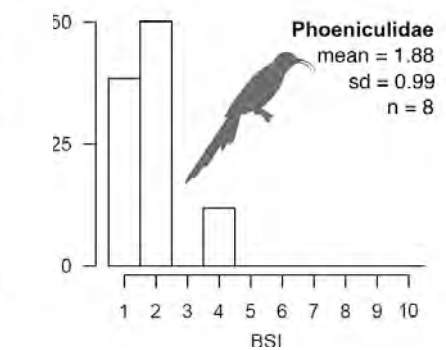
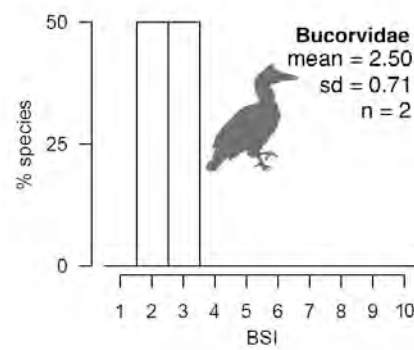
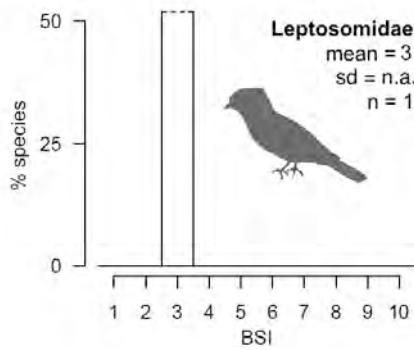
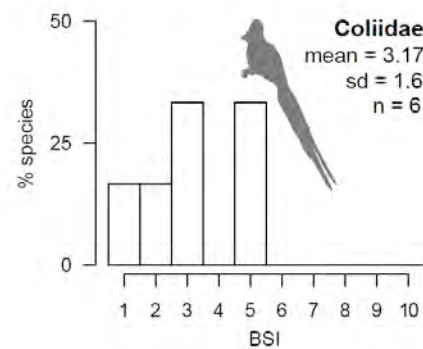
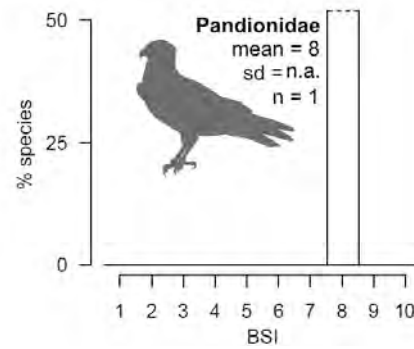
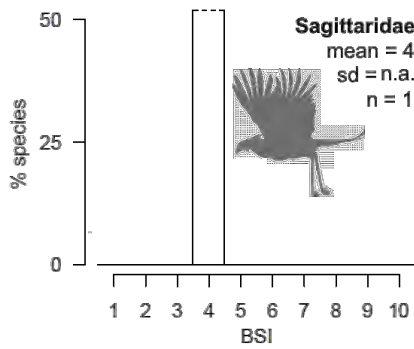
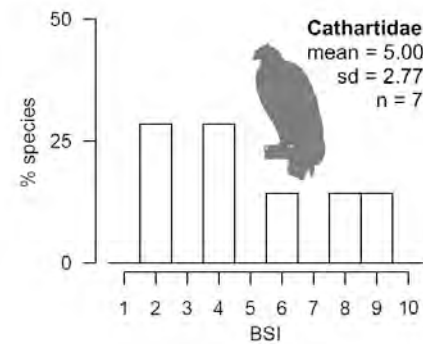
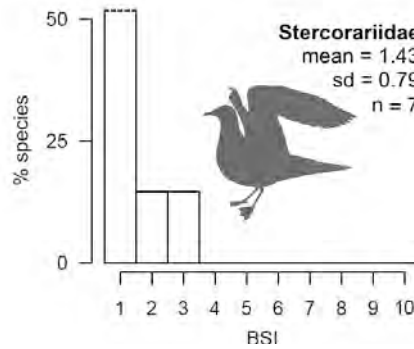
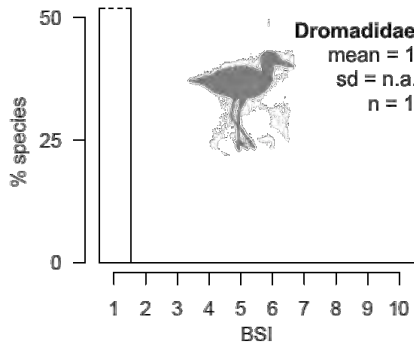
2. Biomic specialization



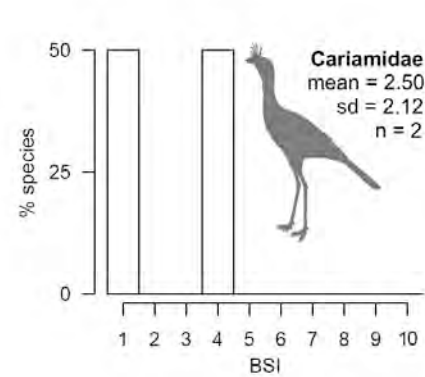
2. Biomic specialization



2. Biomic specialization

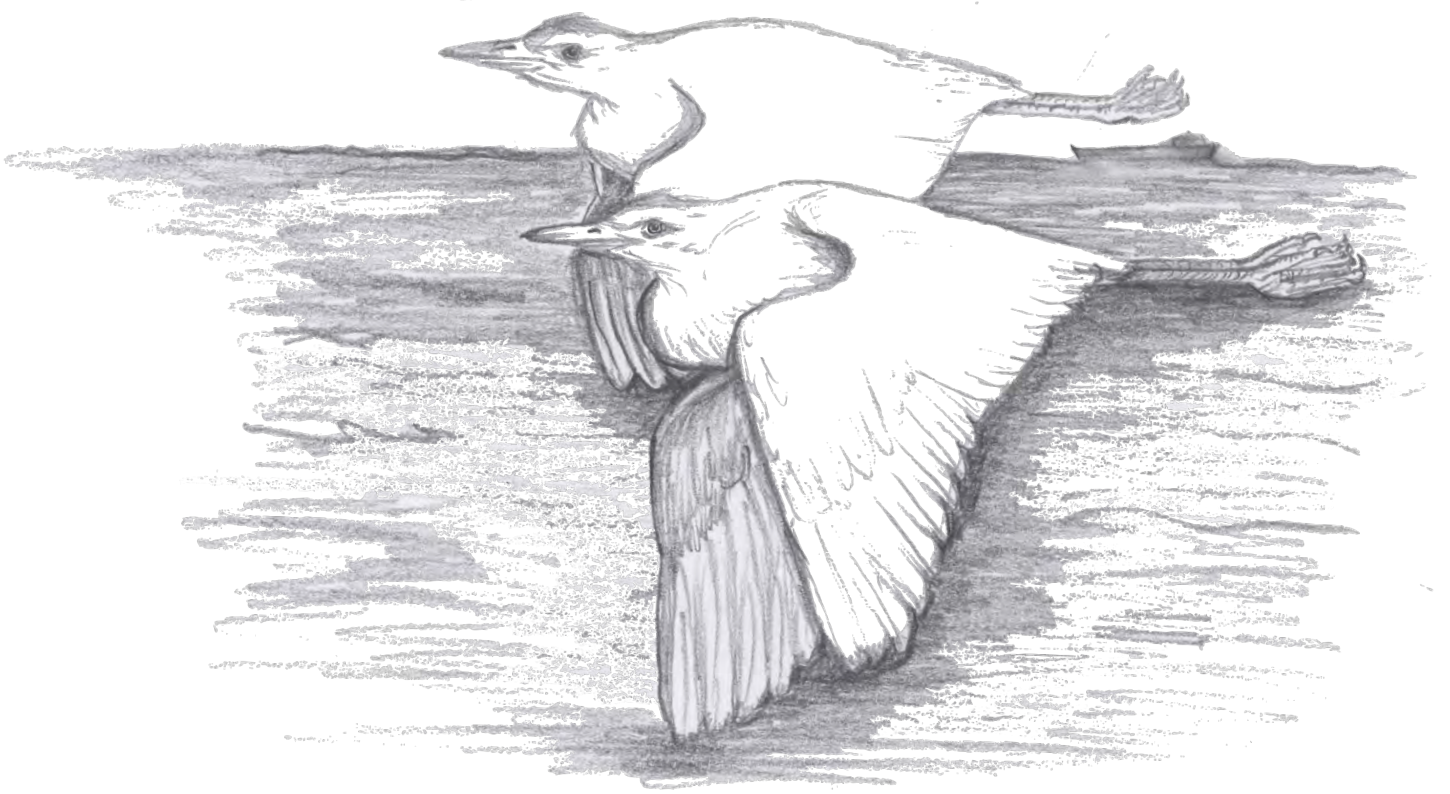


2. *Biomic specialization*



3

Paleobiogeographic history





3

Out of South America: adding fossils and tectonics for a new biogeographic history of modern birds (Neornithes)

“...The animal kingdom developed in Australia shows anomalies and peculiarities perhaps even more extraordinary than the displayed by plants. Nevertheless, since the dispersion capacity of the various groups of animals varies greatly, there is less uniformity in the phenomena they present.”

Alfred Russel Wallace (1893)

"The extreme rarity of transitional forms in the fossil record persists as the trade secret of paleontology. The evolutionary trees that adorn our textbooks have data only at the tips and nodes of the branches; the rest is inference, however reasonable, not the evidence of fossils."

Stephen Jay Gould (1941-2002)

ABSTRACT

Birds are one of the most specious groups of terrestrial vertebrates and inhabit all the ecosystems of the Earth. This adaptive success is related without doubt to the development of a prominent fly capacity. This trait allowed that early birds reached an important dispersal capacity and colonized diverse novel environments. With the aim of reconstructing the most probable biogeographic scenario of the origin and early diversification of birds, we considered diverse roles of dispersal capacity to explain the

3. *Paleobiogeographical history*

large-scale geographic patterns showed by Neornithes lineages. Bird evolution in a geographic context was reconstructed based on their phylogenetic relationships, taking into account paleontological information for the calibration of divergence processes. We also considered ancestral taxa as well as tectonic and paleoclimatic information. According with our results, we propose a Neornithes origin in South America. The most probable evolutionary model implied the role of South America as refugia during the late Cretaceous environmental changes, which allowed the survival of early neornithine birds. Moreover, we propose three main dispersal waves. The first one, during the late Cretaceous protagonized by Palaeognathae, Galloanseres and Aequornithes. Second, there was a great diversification during the Paleocene-Eocene in terrestrial-dwelling lineages (Caprimulgimorphae and Telluraves), which was related with global warming conditions expanding tropical environments. Third, the expansion of niches diversity due to appearance of new marine currents generated by cooling trends along the Oligocene and grassland biomes across the late Oligocene and Early Miocene triggered a new dispersal wave of marine and terrestrial lineages respectively (Charadriiformes, Procellariiformes, Galliformes, Otidiformes, etc). Overall, our results suggest a preponderant role of global climate and tectonics in dispersal and vicariance events configuring the modern distribution and diversity of bird families. In spite of the incompleteness of the avian fossil record, this approach indicates the importance of integrate all the available information to postulate a holistic model for bird evolution within a deep-time scale.

Key words. Birds, dispersal-extinction-cladogenesis (DEC) analysis, historical biogeography, paleobiogeography, Lagrange.

3.2. INTRODUCTION

Birds (Aves), with near 10,000 living species, are one of the most specious clade of terrestrial vertebrates (Gill 2007; Jetz et al. 2012; Del Hoyo and Collar 2014). They are spread across all continents and a wide array of environments, being the result of an extraordinary radiation that spans since the late Jurassic —when they evolved from derived Theropods— to the striking variety of ecological and morphological adaptations that they currently hold (Chiappe and Witmer 2002; Zhou 2004). Our

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knowledge of their current biology, ecology and distribution is vast, and growing paleontological evidence is clarifying key morphological steps of their evolutionary history (Mayr 2009, 2014b; Ksepka and Boyd 2012). However, we require an understanding of the deep-time context of such radiation to clarify the possible relationship between historical events and their current geographic distributions.

The evolutionary relationships of modern birds (Neornithes) at higher level (orders and families) are now relatively well established due to molecular and morphological studies (Dyke and van Tuinen 2004; Ericson et al. 2006; Livezey and Zusi 2007; Hackett et al. 2008; Pacheco et al. 2011; Jetz et al. 2012; Lee et al. 2014; Jarvis et al. 2014). Some of these phylogenetic approaches were dated with paleontological information suggesting that stem groups of modern lineages arose during the Upper Cretaceous and diversified around or soon after K/T limit. Furthermore, some authors argue that basal emergence of Neornithes happened in Gondwana before the Cretaceous-Palaeogene boundary (Cooper and Penny 1997; Cracraft 2001; Hope 2002; Longrich et al. 2011; Ericson 2012; Mayr 2014b). The evidence seems indicate that vicariance events during the Gondwana break up leaded the initial patterns of diversification in southern continents with subsequent dispersal events to the northern hemisphere (Cracraft 2001; Ericson et al. 2002; Ericson 2012). The mapping of phylogenetic relationships in groups such as Ratites (van Tuinen et al. 1998; Baker et al. 2014), Galloanserae (Crowe et al. 2006; Frank-Hoeflich et al. 2007), and Telluraves (Australavis and Afroaves) (Ericson 2012) are consistent with this model. All these clades present an evolutionary pattern explained by Gondwana drifting process during the Late Cretaceous (Cracraft 2001; Barker et al. 2004; Ericson 2012; Baker et al. 2014). Nevertheless, some conclusions generates debate because just a few clades are present in the late Cretaceous fossil record, and the oldest fossils of basal groups such as Paleognathae have only Tertiary record (Mayr 2009). The only bird groups with unambiguously fossils in the Cretaceous are Galloanseres and Aequornithes (Feduccia 2003; Clarke et al. 2005b; Ksepka and Boyd 2012; Ksepka et al. 2014; Mayr 2014b).

The continental drift theory was an important conceptual basis to understand the Earth dynamics (Wegener 1912). This theory explained many geographic patterns observed for diverse taxa worldwide and has provided an important support for evolutionary mechanisms such as vicariance and dispersion in biogeographic analyses

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(Cracraft 1973; Ronquist 1997; Zink et al. 2000; McDowall 2004; Limolino et al. 2010; Contreras-Medina and Luna-Vega 2012). The historical variation of connections between landmasses and the climatic changes influencing sea levels were processes that promoted vicariance or dispersion scenarios due to the appearance/disappearance of geographic and ecological barriers (Cracraft 1985; Cox 2000; Voelker 2002; Ree and Smith 2008; Springer et al. 2011; Hawkins et al. 2012; Condamine et al. 2013). Considering this, it is reasonable to think that distribution patterns and bird lineage diversity has been influenced by historical geologic processes. Some approaches in birds biogeographic reconstructions are usually limited in taxonomic scope (encompassing families or subfamilies), use ecological rather than geographic areas (for example, biogeographic zones realms instead of continents, which implicitly assumes that those areas existed throughout the entire time interval of analysis), do not include fossil information, or exclude the changing geographic configurations of landmasses through time in the analyses (Ericson 2012).

In this research we integrated an extensive data source from molecular phylogenies and paleontological studies with geological and climatic information within a historical context. This allowed us to develop an integrative macroevolutionary model that explains bird evolutionary patterns in relation with geographical origin of avian lineages and the influence of historical processes in bird evolution.

3.3. MATERIALS AND METHODS

3.3.1. Phylogenetic hypothesis

Paleobiogeographical reconstruction requires a robust, highly resolved, and time-calibrated tree (Ree and Smith 2008). Considering this, our study constructed a phylogenetic hypothesis based on Jarvis et al. (2014) for high-level clades and Jetz et al. (2012) at the family level. We also used additional information from the phylogenetic hypotheses based on molecular data of nuclear DNA analysis formulated by Ericson et al. (2006) and Hackett et al. (2008). Subsequently, we included the information of fossil birds with relatively well-established evolutionary relationship with respect to modern taxa (Mayr 2009, 2014b; Ksepka and Boyd 2012) (Table S1). We built a consensus tree that contains 215 bird clades (Fig. S1-S4 in Appendix 3.8): 100 non-passerine taxa and the Basal-Passeriformes clade, 43 extinct taxa that presented

phylogenetic information respect to recent families, and 70 fossil taxa used as *stem-clades* and points of calibration for divergences between clades (Table S2). The consensus tree was dated with the package Paleotree in R (R Development Core Team 2013). The fossil presence of ancient taxa also allowed the inclusion of ancestral occupation (AO) information in the analyses for clades that today present a different distribution with respect to the past. For example, the Hummingbirds (Trochilidae) inhabit nowadays New World environments, but fossil evidence indicates that they were present in Europe during the Paleogene (Mayr 2005a; Mayr and Micklich 2010).

3.3.2. *Historical biogeographic analysis*

Several considerations were taken into account to define our biogeographic analysis. First, the planet was divided into ten geologic units based on the tectonic history (Scotese et al. 1999; Scotese 2001): South America, North America (including Greenland, Central America and West Indies), Africa (including Arabia), Europe (considering from western Europe to the ancient Turgai sea way and the recent Urals mountains limits), Asia (from Ural mountains to Japan and from Siberia to Indochina and Sunda islands), India (Indian subcontinent and Tibetan plateau), Antarctica, Australasia (Australia, New Guinea, and Melanesian islands), Zealand (New Zealand and neighbour islands) and Malagasy region (Madagascar island and surrounding archipelagos) (Fig.S5). The distribution data of recent clades was registered as presence/absence in each area considering as criteria that the species of family occupied more than 30% of area. For lineages with marine distribution we considered the same criteria applied to their breeding area in the coast. In the case of the extinct lineages and the *stem*-groups, their ancestral occupation (AO) was coded with geographical data from the fossil record, according with their early apparition (Table S1 and S2). Marginal distributions (<30%), or expansion due to human activities were excluded due to these occupancy records are relatively recent and represent colonizations of punctual species that may affect the inference of origin areas at basal family level (Ree and Smith 2008; Condamine et al. 2013).

3.3.3. *Paleobiogeographic analysis*

For the reconstruction of the geographic origin and dispersal routes of bird lineages during their diversification through time we employed the Dispersal-Extinction-Cladogenesis model (DEC) developed by Ree & Smith (2008). This method describes

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transitions (ancestor-descendant) between geographical areas by interaction of three evolutionary processes: dispersal, local extinction (range contraction) and cladogenesis (vicariance). DEC method calculates the likelihood of each clade range as function of dispersal and extinction rates and estimates global rates of dispersal and extinction given all possible ancestral states at internal nodes. The analysis assumes those rates as constant to calculate the relative probability for geographic ancestral ranges in each one of the nodes along the phylogenetic hypothesis (Ree and Smith 2008; Condamine et al. 2013). The DEC analysis were performed using Lagrange in the program RASP 3.03 (Yu et al. 2011; Yu et al. 2015). Among their advantages, the use of DEC model allows that a specific clade may be present in more than one area or geographic range. Additionally, it generates stratified models, where distinct geographical connections are configured in relation to specific time slices of the analysis interval. According to this, we divided our paleobiogeographical model, which covers a temporal frame of 90 million years ago (since the upper Cretaceous to present), in 30 temporal intervals defined by geological, paleoclimatological studies and information based in intercontinental biotic interchanges in taxa such as mammals or plants (Fig.S5), the time span of these time slices varied between 1 and 5 million years. Following the method (Ree and Smith 2008), we established temporal constraints on the dispersal rates between areas; these constraints were based on the relative position of continents through time (references in Fig.S5). We defined four evolutionary models with specific constraints on the dispersal rates; each model was defined taking into account the possible dispersal rates between areas according with their relative position, geological barriers, land bridges presence and the distance between areas in each time bin. Considering this, we configured each model for the 30 time slides as follow: In absence of any barriers, the dispersal rate between adjacent areas was established as 1.0 for all the models. Then it was created three different configurations where the dispersal rates between landmasses separated by a maximum of 2,000 km were set to 0.5, 0.25 and 0.1 (for instance, Africa and Madagascar or Australia and New Zealand today). This 2,000 km limit was established in the remotest island colonized by birds (Tristan da Cunha Islands)(Holdgate 1965). Finally, we used two dispersal rates between landmasses further than 2,000 km: 0 or 0.1 (Condamine et al. 2013). According to these, the models were defined as: 1-0.1-0 Model, 1-0.5-0 Model, 1-0.25-0.1 Model and 1-0.5-0.1 Model (from the most conservative to the more flexible setup).

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Using 10 areas would translate into 1024 (2^{10}) possible area combinations. This is beyond the DEC model computational limit and, we constrained the occupancy of certain areas combinations because the relative position of some continents suggest biological implausibility (Ree and Smith 2008; Condamine et al. 2013). Likewise, the different clades of birds present clear differences in their flying capacity and dispersal (De Queiroz 2005; Thorup 2006; Rolland et al. 2014; Pelegrin et al. 2015). For this reason and for computational viability, we carried out specific analyses to reconstruct the ancestral area in each one of 10 high-level clades according with Jarvis et al. (2014) (Palaeognathae, Galloanseres, Columbea, Otidimorphae, Caprimulgimorphae, Gruiformes, Charadriiformes, Aequornithes, Afroaves and Australaves), and evaluate their evolution under each dispersal scenario. Finally, with the results for each clade we performed a general analysis for Neornithes considering the diverse models. The optimal root area proposed by the model that better explains the distribution patterns was determined by comparison between likelihoods scores in each model considering significant differences when final likelihood score (f) was greater than or equal to two log-likelihood units, for $-\ln L$ values this implied lowest values (Condamine et al. 2013).

The reconstruction process of biogeographic ancestral occupancy combines all the information (living species geographic distribution, the tree topology, fossil record of recent and extinct lineages and the availability of connections among continents through time) and yields the likelihood values for each biome combinations in each node. Lagrange output for ten-areas analyses is complex. In order to organize the results and obtain the general paleobiogeographic patterns, we established a criterion based in the selection of the continent configurations with highest probability results for each node, which were organized decreasingly according to their likelihood value. The probability scores for these landmasses combinations were cumulative until a value of 0.5 was reached. The relative likelihood scores of each continent within these combinations were summed and all continents with a cumulative likelihood of more 0.25 were retained for each node (Tables S3-S14). For example, if for a node the most probable landmasses combinations are ST (presence in South America and Antarctica) with a likelihood value of 0.35, and SN (presence in South America and North America), with 0.15, this would imply that the values of relative probability for each continent are defined as follows: T= 0.35, S=0.50 and N=0.15. We would then

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consider that only landmasses S and T are robustly reconstructed for that particular node.

According to the likelihood values for each model, we selected the optimal model to explore the colonization dynamics along the avian evolution in each continent. Then, we established the colonization events that explain the nodes states along the branches of the tree; the colonization events inferred by recent and extinct groups (considering fossil evidences) were integrated together. However, these events have a temporal uncertainty related with the moment of colonization, which might have happened in any instant along the branch or, in the case of fossil branches, their presence indicates the upper limit of possible colonization. Likewise, the phylogeny presents a trend to increase the amount of branches along time producing an important bias towards present. To solve this, we analysed the continental colonization through time using a sliding window method (Meredith et al. 2011; Wang et al. 2012). Through this approach we calculated the mean and the confidence interval of colonization rate from/towards each continent in 1 million years time intervals and smoothed with a 5 million years sliding window that considers the proportion of lineages in each period.

3.4. RESULTS

The likelihood scores and the root occupancy reconstructions for the four different evolutionary models are summarized in Tables 1 and 2. Detailed paleobiogeographical reconstructions for each clade under each model are shown in Fig. S1-S4 and the likelihood estimates for each node with their relative values until 50% in Table S3 to Table S13 (Appendix 3.8). The results for Neornithes (tree root) showed that less restrictive scenarios for dispersal (1-0.25-0.1 and 1-0.5-0.1 models) presented the highest likelihood values without significant differences. The 1-0.5-0.1 model presented highest likelihood values in 7 clades, while the 1-0.25-0.1 model showed high likelihood in only 2 clades. However, there were statistical similarities among models for diverse groups. For instance, in Palaeognathae, Gruiformes and Australaves, the 1-0.5-0.1 model do not differ significantly from the 1-0.5-0, whereas for Galloanseres, Columbea and Caprimulgimorphae the 1-0.25-0.1 model was statistically similar to 1-0.5-0.1 model. Finally, all the models performed similarly in

Otidimorphae. Due to the statistical significance and the higher likelihood values in the majority of groups, we chose the 1-0.5-0.1 model as the most representative model. Fig. 1A and 1B, summarized our findings and colonization events following this model (1-0.5-0.1). This model proposes an origin of Neornithes in South America. Despite the likelihood differences, other scenarios such as the 1-0.25-0.1 and 1-0.1-0 models also proposed South America or Gondwana respectively as the origin area and possible centre of radiation for Neornithes.

The pattern of historical occupancy and dispersals remained similar across clades and models (Table 2). Our results suggest that ancestors of Otidimorphae and Australaves presented an initial diversification in the Southern Hemisphere, while the ancestors of other bird lineages would have diversified after colonizing the Northern Hemisphere. According with the best model, different pulses of colonization events to North America from South America during the late Cretaceous made possible the subsequent expansion of basal lineages across Asia. Furthermore, the South American proximity with Africa and Antarctica probably allowed the colonization and evolution in these continents and the subsequent expansion towards Europe across Africa, and to Australia and Zealand from Antarctica. This pattern suggests that during the initial evolutionary history of birds, North America, Africa and Antarctica probably were used as dispersal routes towards Asia, Europe and Australia respectively (Fig. 1A and 1B.).

The analysis of colonization rates (Fig.2) for each continent showed a high colonization rate of North America, Europe, Africa and Zealand during the first half of the upper Cretaceous. Other continents such as Australia, India and Madagascar presented peaks in their colonization patterns around 80 Ma. Conversely, Asia and South America presented low colonization rates during this period. In spite of their differences, all the continental patterns reflected a substantial decrease in the colonization rates around the latest Cretaceous, except for South America. During the Paleocene there were important stages of increasing colonization rate, which were intensified further during the early Eocene. Finally, around the Oligocene-Miocene boundary were registered new maximum values for colonization rates in all the continents.

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Table 1. Likelihood for paleobiogeographic analyses ($-\ln l$) i =initial likelihood; f =final likelihood for the bird clades in each evolutionary model. Bold numbers are the lowest values of $-\ln L$ (high probability). Red values don't present significant differences respect to the lowest values, the significantly support was considered when differences greater than or equal to two log-likelihood units (Ree and Smith 2008).

Clade	1-0.5-0.1	1-0.25-0.1	1-0.5-0	1-0.1-0
Palaeognathae	$i=31.38$ $f=30.51$	$i=32.74$ $f=32.21$	$i=30.28$ $f=28.89$	$i=34.73$ $f=32.05$
Galloanseres	$i=114.87$ $f=113.56$	$i=118.30$ $f=115.01$	$i=124.79$ $f=120.01$	$i=145.24$ $f=128.69$
Columbea	$i=58.98$ $f=55.01$	$i=60.72$ $f=54.45$	$i=71.59$ $f=59.53$	$i=86.57$ $f=62.44$
Caprimulgimorphae	$i=79.66$ $f=77.75$	$i=82.62$ $f=78.85$	$i=88.36$ $f=83.10$	$i=104.76$ $f=90.72$
Otidimorphae	$i=29.05$ $f=22.14$	$i=31.23$ $f=21.94$	$i=31.85$ $f=22.43$	$i=39.86$ $f=22.84$
Gruiformes	$i=65.82$ $f=62.86$	$i=69.94$ $f=64.93$	$i=68.60$ $f=63.06$	$i=81.80$ $f=70.20$
Charadriiformes	$i=150.80$ $f=146.46$	$i=158.98$ $f=149.94$	$i=165.68$ $f=152.71$	$i=201.22$ $f=169.08$
Aequornithes + Phaethontimorphae	$i=231.54$ $f=218.21$	$i=244.24$ $f=222.00$	$i=284.65$ $f=245.21$	$i=359.03$ $f=273.22$
Afroaves	$i=241.596$ $f=239.164$	$i=254.078$ $f=248.211$	$i=257.082$ $f=247.633$	$i=308.383$ $f=277.578$
Australaves	$i=77.18$ $f=72.98$	$i=82.02$ $f=75.61$	$i=88.81$ $f=73.09$	$i=112.66$ $f=83.30$
Neornithes	$i=92.12$ $f=87.42$	$i=97.57$ $f=87.31$	$i=112.44$ $f=95.65$	$i=144.73$ $f=102.91$

Table 2. Areas defined for bird high-clades according with the four evolutionary models used. (A= Asia; E= Europe; F= Africa; I=India; M= Madagascar; N= North America; S= South America; T = Antarctica; U= Australia; Z= Zealand). For more details about the data and analyses see Supplementary Tables in Appendix 3.8.

Clade	1-0.5-0.1	1-0.25-0.1	1-0.5-0	1-0.1-0
Palaeognathae	NE SZF	N SZF	N SZF	N SZF
Galloanseres	NE SU	NE SU	NE SU	NE SU
Columbea	E SUM	E SUM	SFUM	SUM
Caprimulgimorphae	E S	E S	E S	EA S
Otidimorphae	SFIM	SFIM	SFIM	SFIM
Gruiformes	NE SFZ	NE SFZ	NE FZ	N SZ
Charadriiformes	NEA SFU	NEA SFU	NEA SFU	EA SFU
Aequornithes + Phaethontimorphae	NA STZ	N STZ	N STZ	N STZ
Afroaves	E F	NE F	E F	E F
Australaves	STU	STU	STU	STU
Neornithes	S	S	NEA SFT	STUZ

3.5. DISCUSSION

3.5.1. *Origin and early diversification in Neornithes.*

The development of a prominent flying capacity in early birds during the beginning of their evolutionary history allowed them to move efficiently across diverse environments and to avoid ecologically hostile conditions respect to other land animals (Chiappe and Dyke 2006). Moreover, the evolution of long-distance dispersal capacities was key in the dispersal of bird lineages through continents. This is agreement with our results, which suggest models with higher dispersal rates (1-0.5-0.1 and 1-0.25-0.1) as the better-fits to the data. The differences observed in the likelihood values for the clades probably have relationship with the development of an aerodynamic morphology and diverse physiological mechanisms for the flight energy efficiency (Hedenström 2010), which depends on each clade historical particularities. These characteristics and different dietary specializations possibly constituted as important adaptations for the evolution of diverse flight strategies allowing the initial morphological and ecological differentiation between avian lineages (Mitchell and Makovicky 2014). Likewise, these traits would have constitutes as exaptations (Gould and Vrba 1982) for achieved prominent dispersal capacity over long distances and even during independent moments of the avian history allowing the evolution of migratory behaviour (Alerstam et al. 2003; Piersma et al. 2005).

The models with highest probabilities estimate the origin of Neornithes in South America during the Upper Cretaceous (about 101 Ma), which is in line with fossil evidences (Agnolin and Novas 2012). The results showed an evolutionary scenario with diverse colonization events from South America during the upper Cretaceous. These patterns probably are related with the initial proximity between South America and the other Gondwanan landmasses enabling their colonization by early lineages and their succeeding expansion. Gondwana started its break around 180 Ma (Scotese et al. 1999) and the effect of plate tectonics in the configuration of landmasses determined the arising of many vicariance processes and opportunities for biotic exchange in the southern continents (Rage 1988; Cracraft 2001; Givnish and Renner 2004; Limolano et al. 2010). In this way, the relative closeness and the continuous fragmentation process probably were key factors in the colonization processes of early lineages with different

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dispersal capacities, which allowed parallel evolution and different diversification patterns (Claramunt et al. 2012).

3.5.2. *Palaeognathae historical biogeography*

Considering the Palaeognathae early evolution (Fig.1A), our findings showed a dispersal process along the upper Cretaceous reaching a broad distribution towards Africa and Zealand in Southern latitudes, as well as North America and Europe. About 100 Ma Africa separated from South America and during this time probably the ancestors of African and Northern Hemisphere ratites invaded Africa (Ezcurra and Agnolin 2012). Furthermore, land connection between South America and Antarctica persisted until the Drake opening during the late Eocene and probably many lineages may colonized Zealand during the middle Upper Cretaceous through Antarctica (Laird and Bradshaw 2004). According to this, our findings are consistent with the Gondwanan origin and diversification of Ratites (van Tuinen et al. 1998; Cracraft 2001; Johnston 2011) with successive colonizations of the Northern Hemisphere during diverse periods. These colonizations probably were possible for medium-size lineages that reached Europe via Africa and further North America using the De Geer route (Brikiatis 2014). This is evidenced in the Northern Hemisphere by the presence of extinct ratite lineages such as Palaeotididae and Lithornithidae in Northern Hemisphere (Mayr 2009; Stidham et al. 2014b). For the case of Lithornithidae, diverse anatomical features have suggested that probably had the ability to perform sustained flight associated to a semi-aquatic niche (Houde 1988; Mayr 2009). Which is also consistent with convergent development of flightlessness from flying ancestors during ratites history due probably to the isolation and low predation pressure (Phillips et al. 2009; Baker et al. 2014).

3.5.2. *Galloanseres historical biogeography*

During the Upper Cretaceous, Galloanseres ancestors dispersed across North America, Europe and Australia (Fig.1A). The colonization process from South America to North America might allow the further colonization of Europe using the De Geer route and land bridges that connected the Euramerica stage (Sanmartín et al. 2001; Pereda-Suberbiola 2009; Ezcurra and Agnolin 2012). Likewise, Antarctica probably was an important route towards Australia. The broad extension that early Galloanseres reached in the Northern and Southern Hemispheres suggest that extinct lineages such

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as Pelagornithidae already had an important fly capacity (Mayr 2011a). Recent groups such as Anseriformes have even developed migratory behaviour, which has been key in their evolutionary success (Dalby et al. 2014). The isolation process in two continental scenarios could make possible the vicariance and evolution of Galloanserae basal forms (Gastornithidae and Pelagornithidae) and the subsequent evolution of Galliformes in the Northern Hemisphere (Mayr 2009), while Anseriformes ancestors expanded across the Southern Hemisphere, evolving in South America and Australia. This is in agreement with the presence of Anseriformes fossil evidence in Antarctica (Clarke et al. 2005b), and the prominent presence of basal lineages of Anseriformes in the Southern Hemisphere, such as Anhimidae, Anseranatidae and Dromornithidae families (Murray and Megirian 1998; Alvarenga 1999). In the Anatidae case, basal groups such as Dendrocygninae, and diverse tribes such as Malacorhynchini, Stictonettini, Cereopseini also occur in the Southern Hemisphere (Eo et al. 2009; Del Hoyo and Collar 2014). We observed an early dispersion of Anseriformes towards the Northern Hemisphere during the Paleocene, while early Galliformes were restricted to Europe forests during the Paleocene. These patterns may propose a biogeographic history related with the development of flying and body size specializations. In the case of Gastornithidae and Pelagornithidae, the differentiation in niche preferences by body size probably drove to the divergence process between their ancestors from the other Galloanseres, these lineages reached large body sizes with land and aquatic life respectively (Angst et al. 2014; Ksepka 2014). On the other hand, Galliformes in the Northern Hemisphere might have adapted to the forest life style and probably have evolved towards flightlessness condition (Mayr 2009) caused by the absence of larger terrestrial predators after the extinction of dinosaurs (van Valkenburgh 1999; Mayr 2009). These conditions, and the tropical island environments in Europe might have triggered the basal diversification of Galliformes in many stem lineages during the Paleocene (Mayr 2005b). Meanwhile, the Anseriformes probably preserved the flying capacities associated probably with a semiaquatic lifestyle, which enabled them to disperse from the South Hemisphere to North America and Eurasia during the latest Cretaceous and Paleocene (Kurochkin et al. 2002; Mayr 2009). Finally, in Galliformes the colonization events by crown clades towards southern continents would be later to the basal radiation in the Northern Hemisphere. Diversification of modern crown lineages during the late Eocene and Oligocene probably was triggered by the climate changes that transformed the warm and forested global environments in cooler,

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seasonal and arid habitats (Zachos et al. 2001; Edwards et al. 2010), which may favoured their diversification in the Old World and North America (Mayr 2005b, 2009; Mourer-Chauviré et al. 2011) (see more discussion and details in Chapter 3). Therefore, our findings for crown Galliformes are inconsistent with the Gondwana break-up as predominant mechanism that promoted the vicariance and evolution in Galliformes as proposed by Cracraft (2001).

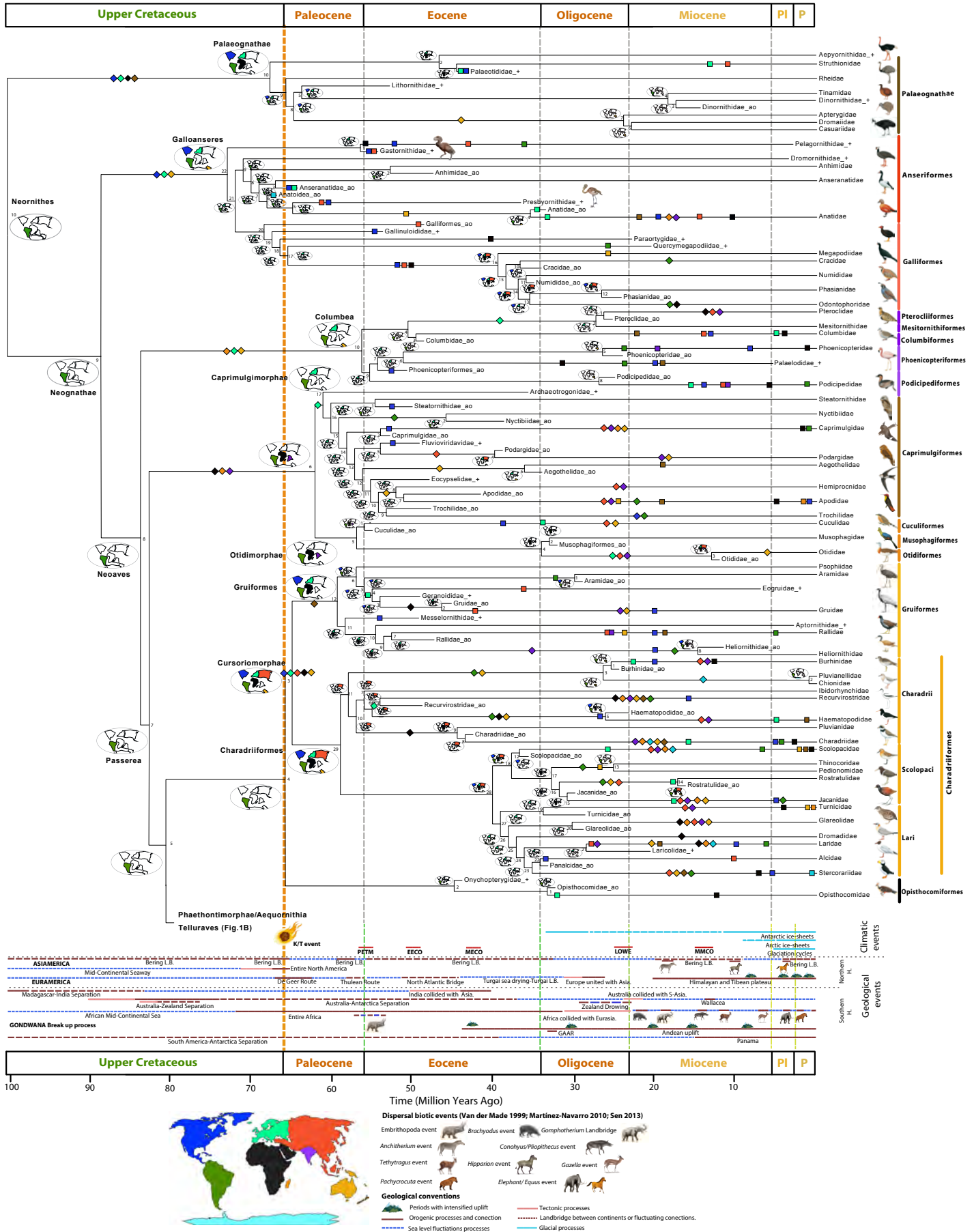
3.5.4. *Columbea historical biogeography*

During the latest Cretaceous, different dispersal episodes from South America enabled a broad geographical distribution in diverse ancestors of Neoaves clades. Due to subsequent isolation, these clades diversified by parallel evolution in diverse lineages adapted to the particular conditions of each continent. Columbea evolution presented an initial dispersion from South America towards Europe and Australia during the upper Cretaceous. This reconstruction suggests a possible dispersal route through Africa and Antarctica. The dispersion across Africa and Madagascar is evidenced also in Caprimulgimorphae and Otidimorphae ancestors. These patterns seems to indicate that during the latest Cretaceous and the Paleocene, Africa played an important role as a dispersion route from South America towards Europe (Ezcurra and Agnolin 2012), where Columbea ancestors developed a significant diversity along the Paleocene and Eocene (Mayr 2009). These findings are consistent with interchange events reported in mammals such as the Embrithopoda event (Sen 2013).

Phoenicopterimorphae evolution was associated with an isolation process in Europe respect to Australia, this process might generated an important diversity of flamingo-like species (Mayr 2009, 2014a), probably associated to aquatic and semiaquatic conditions in the tropical and insular Eocene Europe (Mayr 2011c).

Figure 1A. Paleobiogeographical patterns in Neornithes according with the 1-0.5-0.1 Model using Lagrange (DEC). The continental colonization events that explain the inferred area(s) with the highest relative likelihood (in the nodes) respect to present-day distributions is indicated by coloured rhombus and squares. Rhombus, in the middle of the clade indicate the theoretical colonization, if exist fossil supports for events, these are indicated with squares according to the fossil calibration and date (see references in Appendix 3.8. Table S1 and S2).

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Conversely, the early evolution of Columbimorphae was structured by the development of Columbiformes lineages in South America and Australia, and Pterocliiformes in Europe. The relictual presence of Mesitornithiformes in Madagascar, sister group of Pterocliiformes, is an interesting indicator of the Old World evolution of this clade. The southern evolution of Columbiformes is consistent with the broad presence of basal lineages in South America (Johnson and Clayton 2000a, b) and the prominent diversification that doves present in Southern Pacific islands near Australia (Cibois et al. 2014). On the other hand, Pterocliiformes would have dispersed from Europe to Africa and Asia during the Neogene probably in concomitancy with many interchange events reported in mammals (van der Made 1999). These findings agree with the adaptation of Pteroclididae species to arid conditions (Hinsley et al. 1993), which increased during the Late Oligocene and established the beginning of a generalised aridification process in the Earth (Zachos et al. 2001; Edwards et al. 2010).

3.5.5. Caprimulgimorphae and Otidimorphae historical biogeography

The evolution of Caprimulgiformes was associated with the colonization of Europe by ancestral forms. Our reconstruction suggests that the adaptive radiation of the clade took place in Europe during the Paleocene. The archipelago condition of Europe and its tropical climate might facilitated the diversification of the Caprimulgiformes during the Paleocene and early Eocene (Mayr 2011c), and subsequent dispersion of multiple lineages from Europe towards North America and Asia using the Thulean route (Lindow and Dyke 2006; Brikiatis 2014) or through the Turgai Strait respectively. These colonization events were key in the diversification of Caprimulgiformes taxa across the world. Likewise, the development of a sophisticated flying capacity and even migratory strategies would be crucial in the dispersion of Caprimulgidae and Apodidae worldwide (Barrowclough et al. 2006; Thomassen 2005; Larsen et al. 2007; Päckert et al. 2012).

During the Paleocene and Eocene, European avifaunas evolved in an archipelago with tropical conditions (Lindow and Dyke 2006). Under this scenario occurred the early diversification of Caprimulgiformes lineages (Fig. 1A) (Larsen et al. 2007; Braun and Huddleston 2009). The extinction of European lineages around the Eocene-Oligocene boundary probably was triggered by the confluence of diverse factors such as climatic events (Francis et al. 2008), which affected the plant physiognomy of

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tropical environments in the Northern Hemisphere (Lindow and Dyke 2006) as well as species with high dependency of their resources for feeding or nesting such as Trochilidae, Nyctibidae and Aegothelidae. During this period, some lineages of these families relocated their distribution towards tropical environments in the south of North America and Asia, making possible the ulterior colonization of South America and Australasia respectively. Likewise, the differential extinction of European forms respect to others also might have relationship with the biotic interchange between Asia and Europe during the closure of Turgai Strait. According with Mayr 2011c, during the Grande Coupure turnover (Stehlin 1909) entered in Europe new mammalian taxa such as muroid rodents and carnivorans (felids and viverids), this new predation pressure would have affected significantly the unadapt nesting strategies in European lineages that evolved in isolated conditions (Mayr 2011c). This is also in line with the last occurrence of flightless lineages in Europe (Mayr 2009). This ecological process has been reported in modern insular environments, which the predation by mammals and snakes is the main cause of extinction in avian populations (Blackburn et al. 2004).

Ancestors of Otidimorphae dispersed across South America, Africa, Madagascar and India. Subsequently, our findings propose an early divergence between Cuculiformes and Otidiformes-Musophagiformes, which remained restricted to Africa. Conversely, the wide geographical distribution of the early Cuculiformes allowed their spread towards the Northern Hemisphere. This is in line with the presence of cuckoos with terrestrial habits in Madagascar and Indomalaysian, *Coua* and *Carpococcyx* respectively (Hughes 1996; Posso and Donatelli 2012). These basal lineages probably conserved the terrestrial condition due to long isolation and the low predation pressures that suffer Madagascar and the Indian subcontinent. This relationship between Malagasy and Indian faunas has been observed in many taxa (Yoder and Nowak 2006; Warren et al. 2010). Later, the Indian lineages colonized the Southern Asian habitats when both continents contacted each other. Therefore, the presence of Cuculidae in North America, Eurasia and Australia is a derivate condition, likely due to diverse colonization events from South America, Africa and Southern Asia (Posso and Donatelli 2012), which is consistent with the fossil record for Cuculidae (Baird and Vickers-Rich 1997).

The evolutionary patterns for Otidiformes and Musophagiformes suggest that during the Oligocene both groups diverged in Africa. This process probably is related

to ecological specialization. While the Musophagiformes lineages evolved in close association to forested environments (Turner 1997), the bustard lineages developed adaptations to open and arid conditions (Williams and Tieleman 2001). The increasing aridification since the late Oligocene generated ecosystems such as grasslands and savannas that took preponderance in the landscapes (Zachos et al. 2001; Jacobs 2004; van Dam 2006; Senut et al. 2009), which probably favoured the spread of Otididae across the Old world during the Neogene (Sánchez Marco 1990; Mlíkovský 2002). Meanwhile Musophagidae only entered in Europe during the middle Miocene, probably associated with dry seasonal forested environments (Mayr 2011c).

3.5.6. Opistocomiformes and Cursoriomorphae historical biogeography

Opistocomiformes ancestors evolved restricted to South America with a later colonization of Africa and Europe (Mayr et al. 2011), which indicates that possibly the interchange capacity between South America and Africa persisted until the Oligocene (Ezcurra and Agnolin 2012). Similar biotic interchanges across the Atlantic have been proposed for different taxa, even for animals with a presumable low dispersal capacity, as the ancestors of New World monkeys (Bond et al. 2015), caviomorph rodents (Poux et al. 2006; de Oliveira et al. 2009), as well as diverse fish and lizard lineages (Lundberg et al. 2007; Vidal et al. 2008).

On the contrary, Cursoriomorphae ancestors dispersed from South America, achieving a broad geographical distribution in a relative brief time span just after the Cretaceous – Paleogene boundary (Fig.1A). This suggests an early development of more efficient flying capacity, which probably arose in relation with the adaptation to aquatic and semiaquatic life style and omnivorous dietary habits (Pelegri et al. 2014). Moreover, the K/T event would have affected the occupancy of ecological niches due to the extinction of aquatic birds such as Hesperornithiformes or Ichthyornithiformes restricted to the Northern Hemisphere (Chiappe and Dyke 2002; Clarke 2004; Wilson et al. 2011). Due to the geographical focus of K/T event, probably the climatic changes and their environmental consequences were more intense in northern latitudes respect to Southern Hemisphere (Archibald et al. 2010; Schulte et al. 2010).

The broad distribution reached by Charadriiformes ancestors allowed subsequent vicariance processes and the parallel evolution of different clades in different continents. Despite, the inference difficulties associated to wide geographical

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distributions achieved by many clades along their evolutionary history (Mayr 2011b), fossil evidences and geographical distributions for basal groups shed light on the paleobiogeographical pattern of Charadriiformes. Charadrii diversified during the Eocene in Asia presented later dispersal events in direction to Europe and Australia. Probably, isolation mechanisms favoured the evolution of two main lineages: Recurvirostridae-Haematopodidae-Charadriidae in the Northern Hemisphere, and Burhinidae-Chionidae-Pluvianellidae that diversified during the Late Oligocene in the Southern Hemisphere (Paton et al. 2003; Livezey 2010).

During the late Eocene the Scolopaci lineages diverged in a Northern Hemisphere lineage conformed by Scolopacidae, and a Southern clade that diversified through Africa (i.e Jacanidae) and colonized other Southern territories (Pedionomidae and Thinocoridae) during the Late Oligocene. These patterns coincide with the observed for the Burhinidae clade, which might suggest a key link with Antarctica isolation, global cooling and lower sea levels during the Oligocene (Zachos et al. 2001; Paton et al. 2003; Francis et al. 2008).

The obtain patterns for Charadrii and Scolopaci are broadly consistent with the biogeographical scenario proposed by Livezey 2010, explain the relative high intense effect of global climate changes in the Northern Hemisphere respect to Southern continents. The Holarctic lineages suffered diverse process of southward expansions and northward retreats in their distributions due to climatic changes probably promoting the migratory habits. Meanwhile, the distribution of landmasses in southern latitudes limited the impact of glaciations, except for Antarctica. This polar dichotomy reflected the relative abundance and diversity of migratory lineages northwards, while in the southern latitudes are predominately resident or short-distance migratory (Livezey 2010).

Lari patterns suggest that the radiation processes of gulls and allies probably took place in Europe (De Pietri et al. 2011). Under this context, the outstanding diversification of different lineages in Lari can be explained considering the environmental context during the middle and late Eocene. During this time, Europe was still an archipelago and existed a connection route between the western Tethys and the Arctic Sea via Turgai Strait, which enabled the establishment of a warm climate in Europe (Rögl 1999). Two factors might play a key role in the diversification of Lari as

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marine birds in Europe. First, during the middle Eocene there were important peaks in diversity of marine fishes (i.e. Tuna lineage), which constituted an important food supply (Near et al. 2013). Secondly, the absence of marine mammals such as seals and sea lions, which did not appear until the late Oligocene (Churchill et al. 2015), allowed the occupancy of sea niches without ecological competition. Therefore, marine environments possibly represented a source of adaptive zones, which favoured process of ecological differentiation and available diversification of major Lari lineages. Laridae and Laricolidae diversification was predominant during the Oligocene and Miocene; while dispersal capacity and generalist diet requirements allowed to Laridae the colonization of all continents during the Miocene (Worthy et al. 2007), Laricolidae remained associated to European marine environments (De Pietri et al. 2011), which suffered substantial changes during the Oligocene and Miocene (Rögl 1999). In relation to Alcidae and Stercorariidae, our results suggest that their split process was triggered by the Eocene-Oligocene climate transition (Smith and Clarke 2014). During this period, environmental changes affected the ocean latitudinal temperature gradients and caused the development of diverse levels of thermal tolerance by Pan-alcidae ancestors (Smith and Clarke 2014). These adaptations allowed them to diversify across the Northern Hemisphere oceans, with Mancalinae lineage towards the northern Pacific (Smith 2011) and Alcinae in the North Atlantic (Mlíkovský 2009; Smith and Clarke 2014). The divergence process of Stercorariidae probably is related with their ecological specialization such as fly-aquatic predator, respect to swimming and diving habits of Alcidae. The Stercorariidae adaptive zone promoted a broad geographic distribution reaching the temperate latitudes of Northern Hemisphere and subsequently colonizing the Southern Hemisphere during the Pleistocene (Ritz et al. 2008). Interestingly, the Northern Hemisphere families in the three charadriiform lineages would have developed migratory behaviour independently (Del Hoyo et al. 1996; Livezey 2010), which was an adaptive mechanism development probably from exaptation-type traits to cope the emergent seasonal regime (Piersma et al. 2005) caused by the global cooling process that Earth experimented since the Oligocene (Zachos et al. 2001).

Paleobiogeographical patterns of Gruiformes showed a divergence process between the New World and Old World lineages. The early evolution of the American lineage (Gruoidea) was associated with the isolation of North America from South

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America. Within this group, the evolution of Psophiidae was constrained to South America (Ribas et al. 2011), meanwhile the diversification of other families took place in North America. Later, Aramidae would remain in North America, recolonizing South America via Panama landbridge during the Miocene (Montes et al. 2015). The colonization of Europe from North America during the early Eocene through the Thulean route (Brikiatis 2014), and successive dispersals toward Asia and Africa allowed the isolation of the lineages. Geranoididae diversified in Europe during the Eocene, while Eogruidae lineage could have colonized Asia across the Bering Landbridge or during the Grande Coupure event (Clarke et al. 2005a; Costa et al. 2011). Likewise, the closeness between Europe and Africa during the Eocene made possible the colonization of Africa by Gruidae ancestors probably during the Embrithopoda event (Sen 2013), consistent with the presence of basal Balearicinae cranes in Africa (Del Hoyo and Collar 2014).

Finally, the Old World lineage (Ralloidea) evolution was associated with African and European warm environments, predominant during the early Eocene (Prothero and Berggren 1994; Lindow and Dyke 2006; Mayr 2011c; Garcia-R et al. 2014). Later, changes in European climate during the Oligocene, confined basal lineages of Rallidae and Heliornithidae to Africa as evidenced by basal Sarothrurinae in Rallidae and *Podica* for Heliornithidae (Del Hoyo and Collar 2014). Likewise clades such as Messelornithidae colonized North America, during parallel periods respect to the European entry of Gruoidea. On the other hand, the isolated presence of Aptornithidae in Zealand suggests an early colonization process associated with the dispersal capacity developed by the cursoriomorpha ancestors. The broad capacity of dispersion in Ralloidea is supported by the high dispersion observed in the Rails, which are present even in the most remote islands of the Pacific, for instance *Zapornia* cranes (Del Hoyo and Collar 2014).

3.5.7. *Phaethontimorphae and Aequornithia historical biogeography*

The clade Phaethontimorphae-Aequornithia presents a great disparity of groups, which achieved a broad geographical distribution, probably related to their adaptation to marine life-style (Cody 1973; Warheit 1992; Davies et al. 2010). Our paleobiogeographic scenario for Phaethontimorphae and Aequornithia clade suggests an early adaptative evolutionary process that began during the upper Cretaceous, and

implies dispersal from South America to Asiamerica (Scotese 2001) and Zealand via Antarctica (Fig.1B). Apparently, the development of high dispersal flying capacity associated with the invasion of aquatic habitats was an important process that promoted the early diversification of Phaethontimorphae-Aequornithia clade before the K/T. In a similar way to Charadriiformes after K/T, these findings are consistent with the importance of dispersal capacities in the evolutionary patterns for aquatic birds suggest by several authors (De Queiroz 2005; Gillespie et al. 2011). This radiation during the middle late Cretaceous is coherent with the outstanding predominance of diverse aquatic and semiaquatic forms for Ornithurae lineages during the late Cretaceous (Chiappe and Witmer 2002; Longrich 2009). Conversely, along this time enanthiornithes birds dominated the terrestrial ecosystems until their extinction during the K/T event (Longrich 2009; Longrich et al. 2011; O'Connor et al. 2011).

Worldwide distribution of early Phaethontimorpha-Aequornithes probably caused that some distant regions respect to the focus of the K/T bolide impact in North America (Schulte et al. 2010) may played a role as refugia of basal lineages. This could explain the extinction of many shore and marine bird species in the Northern Hemisphere as is reported in Hesperornithidae or Graculavidae lineages (Longrich et al. 2011; Wilson et al. 2011), while contrary Southern originated aquatic groups as basal Phaethontimorphae, Gaviiformes and Sphenisciformes-Procellariiformes common ancestors were able to survive, which is also consistent with the observed patterns in Late Cretaceous basal Anseriformes (Clarke et al. 2005b). Likewise, our results suggest that the Ciconiformes-Suliformes-Pelecaniformes ancestor would have survived in Asia refugia.

Phaethontimorphae ancestors diversified in Africa with the arising of Prophaethontidae and Phaethontidae lineages (Bourdon et al. 2005; Mlíkovský 2009), whereas the Eurypigiformes ancestors evolved in South America. The spread of Phaethontiformes across different latitudes would play an important role in Phaethontidae evolution, which achieved a pantropical distribution while Prophaethontidae were restricted to the Northern latitudes where had to cope with the emerging of cool and seasonal conditions during the late Miocene (Zachos et al. 2001) and ecological competition due to the radiation of other marine birds such Laridae (Mayr 2015).

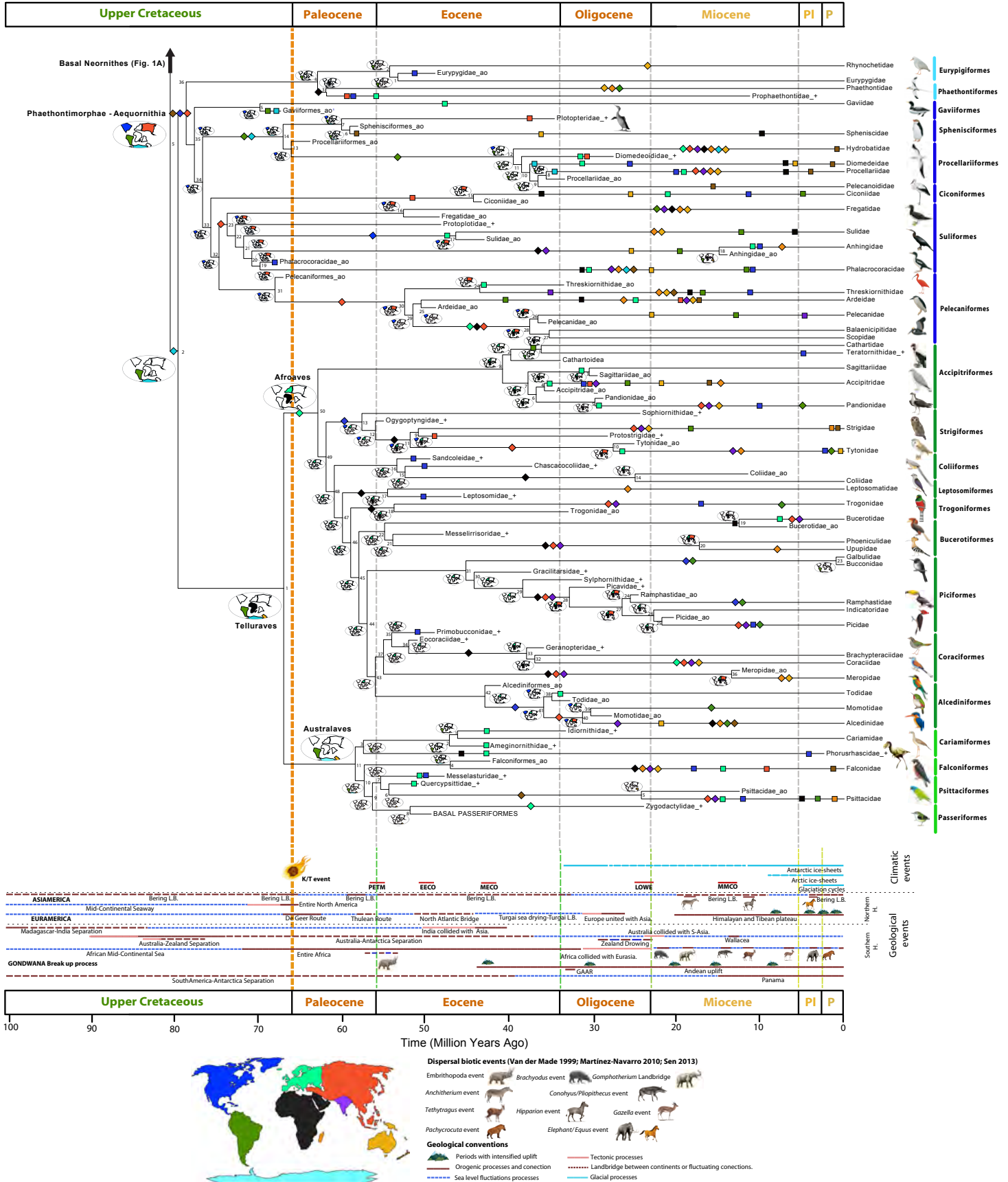
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Early evolution of Gaviiformes, Sphenisciformes and Procellariiformes took place in the Southern Hemisphere associated with different adaptations to the marine life-style (Martin 1995), which separated these three main evolutionary lines (van Tuinen et al. 2001). Gaviiformes colonized the Northern Hemisphere (Mayr and Zvonok 2011) and disappeared from the Southern Hemisphere (Tambussi and Acosta Hospitaleche 2007). Sphenisciformes evolution was focused in the Southern Hemisphere (Ksepka et al. 2006) while Plotopteridae colonized the northern ocean habitats (Olson and Hasegawa 1996; Mayr 2009; Dyke et al. 2011). Early Procellariiformes diversification was mainly restricted to the southernmost latitudes. Some authors propose that the proliferation of isolated environments in islands promoted allopatric processes in the Southern Hemisphere, which influenced on the diversification of Procellariiformes (Chown et al. 1998; Davies et al. 2010). The low dispersion of Procellariiformes towards the Northern Hemisphere along the Paleocene and Eocene was probably due the ecological presence of other lineages with similar niches such as Suliformes, Phaethontiformes or Pelagornithidae, which dominated the marine ecosystems during the Eocene (Bourdon et al. 2005; Bourdon et al. 2008; Mlíkovský 2009). However, lineages such as Diomedeoididae and Diomedidae were able to achieve northern latitudes during the Oligocene (Mlíkovský 2009; Mayr and Smith 2012).

Ciconiformes-Suliformes-Pelecaniformes diversified during the upper Cretaceous in marine environments from North America and Asia (Asiamerica), which was separated from Euramerica through mid-continental seaway (Sanmartín et al. 2001). Under this scenario, during the latest Cretaceous Suliformes diverged from Pelecaniformes probably in relationship with the adaptation to freshwater habitats by Pelecaniformes ancestors in North America, while the Suliformes would remain in Asian sea environments where diversified before K/T probably due to the absence of dominant sea bird lineages such as Hesperornithiformes, which were abundant in the Euramerica and Arctic seas (Rees and Lindgren 2005; Bell and Everhart 2009).

Figure 1B. Paleobiogeographical patterns in Neornithes according with the 1-0.5-0.1 Model using Lagrange (DEC). The continental colonization events that explain the inferred area(s) with the highest relative likelihood (in the nodes) respect to present-day distributions is indicated by coloured rhombus and squares. Rhombus, in the middle of the clade indicate the theoretical colonization, if exist fossil supports for events, these are indicated with squares according to the fossil calibration and date (see references in Appendix 3.8. Table S1 and S2).

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Conversely, the colonization of freshwater environments in North America from marine habitats was promoted probably by the important abundance of these marine lineages (Bell and Everhart 2009; Wilson et al. 2011), due to their presence would implied a possible ecological competence (Rees and Lindgren 2005). Likewise, the freshwater habitats would represent a novel source of adaptive zones and their aquatic morphological traits inhered from their marine ancestors, might constitute preadaptations to subsequent diversification in rivers and lakes (Gould and Vrba 1982). The patterns also suggest substantial differences between the diversification time of Suliformes and Pelecaniformes. This might suggest that Pelecaniformes evolution, which was restricted initially to North America, was affected by the prominent environmental changes around the K/T (Longrich et al. 2011). The colonization of some Asian areas for stem Pelecaniformes made possible that many lineages were able to survive in refugia zones. Subsequently, along the Eocene, the Indian collision with Asia generated the beginning of a continuous process of diverse climatic and geological changes (Chatterjee et al. 2013), which configures new riverine habitats for diversification of early pelecaniform-like lineages. These patterns are consistent with the high richness for freshwater birds in Asia (Buckton and Ormerod 2002), the presence of basal herons (Ardeidae) in Asia (Elzanowski and Zelenkov 2015) as well as the radiation of other bird groups associated with riverine environments such as chats (Turdidae) during the Eocene (Landmann and Winding 1993) and the evolution of ibisbill (Ibidorhynchidae) confined in Asia (Knystautas et al. 1996). Finally, during the Eocene and Oligocene diverse colonization events towards Europe and Africa allowed the differentiation and evolution of Pelecaniformes families, with clades such as Pelecanidae reaching a broad distribution (Louchart et al. 2010; Stidham et al. 2014a) meanwhile others such as Balaenicipitidae and Scopidae remain in Africa (Mayr 2003a).

3.5.8. Afroaves historical biogeography

The paleobiogeographical model obtained proposes a Gondwanan origin for the evolution of Telluraves (Fig.1B). Along the late upper Cretaceous, Telluraves ancestors would have dispersed from South America and Antarctica to Africa and Australia. Likewise, around 66 Ma Australaves and Afroaves diverged each other. Our findings are partially consistent with the “Gondwana break up model”, which explains the evolutionary processes of early bird lineages by isolation between Africa, and South America, Antarctica and Australia (Cracraft 2001; Ericson 2012). However, our

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approach proposes a colonization of Europe from Africa by Afroaves before the K/T event with successive faunal interchange events between these continents during the Paleocene and Eocene. These processes would have been facilitated by the relative closeness between Old World continents (Gheerbrant and Rage 2006; Ezcurra and Agnolin 2012) and the warm climates of Europe during these epochs (Lindow and Dyke 2006; Collinson and Hooker 2003). Europe constituted an archipelago (Rögl 1999) with tropical conditions and island environments that might allow allopatric processes promoting evolutionary radiation (Andersen et al. 2014). Additionally, these environmental features would have conditioned a great diversity of food resources (Collinson and Hooker 2003; Whitfield and Kjer 2008; Condamine et al. 2013). These conditions would have promoted the observed great diversification of European bird lineages. Likewise, these patterns are in line with the European diversification of Caprimulgiformes families, previously commented (Mayr 2003b; Mayr 2005a; Mayr 2009; Mayr 2010).

Considering the African scenario, the development of early Accipitriformes ancestors during the Paleocene might be related to the absence of modern carnivore mammal lineages, which were mainly concentrated in North America and Eurasia (van der Made 1999), as well as the progressive loss of African carnivore lineages such as creodonts and nimravids (van Valkenburgh 1999). In Africa, small-size mammals probably constituted important resources of prey for raptor ancestors (Mayr 2009). Meanwhile, the ancestors of New World vultures would have evolved in Europe with a further colonization of America (Tambussi and Degrange 2013); their extinction in Old World environments might be connected to the development of scavenging habits by some lineages of Accipitridae (Aegypiinae), which diversified during the Miocene as result of growing abundance of herbivore mammals (Zhang et al. 2010). Strigiformes evolved in Europe and colonized North America and Africa in the late Paleocene and early Eocene respectively. Their nocturnal habits would be connected with the abundance of small nocturnal mammals during the Paleocene and the prominent presence of Carnivore mammals in Northern Hemisphere (Mayr 2009). However, also is possible that owls specialized in nocturnal preys due to the competition with the emerging diurnal raptors (Mayr 2009), which colonized Europe and dispersed worldwide during the Oligocene and Miocene, coinciding with the diversification of many rodents and lagomorph groups (van der Made 1999; Dawson 2003; Heissig 2003; Fejfar et al. 2011; Álvarez-Sierra et al. 2013; López-Guerrero et al. 2015).

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Around the Paleocene-Eocene thermal Maximum, which established generalised warm and tropical conditions with temperate forest at highest latitudes (Smith et al. 2006; Röhl et al. 2007; Zachos et al. 2008), diverse interchange events in insectivorous and frugivorous lineages were registered. The presence of land bridges with tropical conditions between Europe and North America (i.e The Geer or Thulean route) favoured fauna interchanges (Sanmartín et al. 2001; Brikiatis 2014). Diverse groups such as Leptosomiformes, Coliiformes and Coraciformes dispersed from Europe to North America (Clarke et al. 2009; Ksepka and Clarke 2010b; Ksepka and Clarke 2010c). Meanwhile, Trogoniformes colonized Africa. During the Oligocene other lineages colonized Africa, Asia and North America, in relation to different geobiological events at the Eocene – Oligocene transition such as the Great Coupure and global cooling (Mayr 2011c).

The broad distribution of Afroaves suggested by our results in Northern Hemisphere environments during the Paleogene suffered an important change during the Miocene that produce the nowadays-biogeographical pattern. The emergence of a highly seasonal global climate regime during the late Miocene limited the food sources along the colder periods in winter. These processes would cause the extinction in northern latitudes of predominantly frugivorous and insectivorous birds such as Coliiformes, or some Piciformes and Coraciformes lineages (Mayr 2011c). Due to these birds probably tended to conserve a relatively narrow physiological thermal tolerance inherited from their tropical ancestors (Ghalambor et al. 2006). According with this, many of these families retracted their distribution towards tropical biomes in equatorial latitudes of the Old and New World (Del Hoyo and Collar 2014).

3.5.9. Australaves historical biogeography

Our findings proposed a scenario in which Australaves ancestor achieved a broad geographic distribution across the southern continents of Gondwana around the Cretaceous-Paleogene boundary (Fig.1B), this implies the divergence from Afroaves through a vicariance process (Ericson 2012) and, therefore, a scenario of convergent evolution of Australaves and Afroaves lineages in diverse ecological niches is reasonable. Predator birds such as Cariamiformes and Falconiformes in South America and Antarctica or Accipitriformes and Strigiformes in Africa and Europe filled faunivorous adaptive zones. Moreover, in Australia took place the evolution of early

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Psittaciformes and Passeriformes, with similar ecological adaptations respect to Afroeurasian lineages such as Trogoniformes, Coraciiformes or Piciformes (Ericson 2012).

During the late Paleocene and Early Eocene the gradual process of separation of Southernmost continents of Gondwana (Sanmartín and Ronquist 2004) promoted the diversification in Australaves. Moreover, the global warming conditions caused that tropical forest extended 10-15 degrees polewards (Jaramillo et al. 2006; Jaramillo et al. 2010), and Antarctica was covered by temperate forests (Poole and Cantrill 2006). This latitudinal climatic gradient conditioned the biomes structure allowing the isolation of some lineages in South America respect to Antarctica and Australia due to ecological specialization in tropical moist and dry forests (Hernández Fernández and Vrba 2005). However land bridges persisted between landmasses, which enabled subsequent dispersal processes in lineages probably more generalist, such as faunivorous Phorusrhacids and basal Falconids, recorded in Antarctica during the Eocene (Tambussi and Degrangé 2013). During the early Paleogene, mammal faunas from South America, Australia and Antarctica were dominated by diverse small body-size lineages of marsupials or animals such as the extinct gondwanatherians (Reguero et al. 2002; Chimento et al. 2015). Conversely, other mammals such as eumammals and notoungulates achieved larger sizes (Reguero et al. 2002; Ortiz-Jaureguizar and Cladera 2006). These mammal assemblages were mainly herbivorous and omnivorous taxa. The carnivorous mammal lineages, highly developed in Northern Hemisphere (van Valkenburgh 1999), were represented only by the sparassodontians in South American ecosystems with a relative low diversity (Prevosti et al. 2013). On the other hand in Australia, the emergence of marsupial carnivorous lineages was during the Oligocene (Glen and Dickman 2014). Under this ecological scenario, the prominent absence of carnivorous mammal species probably was an important factor that promoted the evolution of predator Australaves lineages.

In South America the Cariamiformes lineages would have had a broad ecological success as well as developed a diversity of sizes (Alvarenga and Höfling 2003), which allow them occupy niches as dominant terrestrial hunters in relation with medium and big-size herbivorous preys (Tambussi and Degrangé 2013). The similarities between of small forms (Cariacidae) with African secretarybirds (Sagittariidae) support the process of convergence commented before (Ericson 2012). Likewise, during their evolutionary

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history diverse lineages of Cariamiformes colonized Europe through Africa during the middle Eocene (Angst et al. 2013). This is consistent with the presence of “stepping stones” or the establishment of land bridges by sea level fluctuations, which allowed novel colonization events for land animals as reported for mammal groups (Poux et al. 2006; de Oliveira et al. 2009).

Falconiformes diversified from South America and Antarctica during the Eocene as evidenced by the oldest fossil record for falcon-like species in Antarctica and South America (Tambussi and Degrange 2013), as well as the prominent presence and ecological diversity of basal lineages in Neotropical environments (Fuchs et al. 2011; Fuchs et al. 2012). Probably falcons would have colonized other continents from South America through Africa during the late Oligocene, with a subsequent worldwide diversification during the late Miocene and Pliocene represented by *Falco* species, this adaptive radiation was promoted by establishment and extension of open and seasonal environments such as savannas due to global cooling trends (Fuchs et al. 2015) (see more discussion and details in Chapter 3).

The patterns for Psittaciformes suggest an Australian and Zealander origin, these findings are consistent with the fossil evidence of crown Psittaciformes, as well as the extant presence of clades such as Nestorinae and Cacatuinae (Boles 1993; White et al. 2011). However, there was a significant presence of stem Psittaciformes families in the Northern Hemisphere (Waterhouse 2006; Mayr 2009; Ksepka et al. 2011; Ksepka and Clarke 2012). Stem groups such as Messelsasturidae and Halcyornithidae (Ksepka et al. 2011) presented some anatomical features that resemble to Falconiformes and Strigiformes birds, and even initially classified within these clades (Mayr 2014b). According with this, we postulate a scenario for early evolution of Psittaciformes as predator species along their early diversification consistent with the parallel evolution of Falconiformes in South America and Accipitriformes in Africa and probably promoted by the absence of carnivorous mammals in Australia (Glen and Dickman 2014). This is also consistent with the dietary habits of keas and kakas (*Nestor*), the most basal lineage of crown Psittaciformes (Schweizer et al. 2010) with an important component of predatory habits on other birds and mammals (Del Hoyo et al. 1997), which possibly imply some conservancy of ancestral traits. Under this hypothetical scenario, during the late Paleocene Psittaciformes ancestors in Australia evolved a prominent flying capacity associated with the early predator habits. This trait allowed

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later expansion towards the North Hemisphere across the tropical environments present during the Late Paleocene and early Eocene (Collinson and Hooker 2003) using routes such as the Kerguelen plateau and India (Chatterjee et al. 2013). This is in line with the presence stem parrot fossils such as *Vastanavis eocaena* (Quercypsittidae) from India (Mayr 2009) or *Namapsitta praeruotorum* in Africa (Mourer-Chauviré et al. 2015). Likewise, diverse factors promoted the subsequent extinction of these lineages during the late Eocene such as the climatic changes that occurred in northern latitudes (Mayr 2011c), as well as the possible ecological competence with other emerging raptor groups (Accipitridae and Strigidae). Despite the extinction of stem lineages, the development of high dispersal capacity of Psittaciformes was inherited by derived lineages in Australia, where developed changes in their dietary regime and were able to disperse subsequently worldwide occupying tropical biomes during the Miocene. This prominent parrots dispersal ability is evidenced in the distribution and diversification of many recent lineages in remote islands such as lorikeet species (*Vini*) (Bellemain and Ricklefs 2008; Del Hoyo and Collar 2014). Therefore, this approach is broadly consistent with the patterns of diversification proposed for crown Psittaciformes clades explained by a pulse model from Australia to the southern continents (Schweizer et al. 2010).

Finally, Passeriformes diverged during the early Eocene boundary in association to the broad extension of tropical environments and the diversification of many insects and plants (Collinson and Hooker 2003; Condamine et al. 2013). The divergence of Zygodactylidae as sister taxa respect to Passeriformes might suggest a similar dispersal event to Northern Hemisphere as in stem Psittaciformes. The diversification of other passeriform clades during the early Eocene was located initially in Australia and Zealand. Acanthisittidae, first evolved in Zealand respect to Suboscines and Oscines, which colonized South American and remained in Australia respectively (Ericson et al. 2002; Ericson 2012).

3.5.10. *Paleobiogeographical patterns in Southern and Northern Hemisphere*

The high colonization rates towards North America, Europe, Africa and Zealand during the early and middle Upper Cretaceous (Fig. 2, 3A) are related to lineages that came out from South America. The drifting process of Africa respect to South America implied many vicariance and dispersal possibilities, which were favoured by continental

isolation with a relative closeness of landmasses (Gheerbrant and Rage 2006; Ezcurra and Agnolin 2012) and depended specifically of life-history traits such as the flying capacity of each clade. Colonization of Europe is consistent with the existence of land bridges between North America and Europe (Euramerica) that made possible biotic interchange between both continents (Sanmartín et al. 2001). These land bridges would facilitate the entry of terrestrial and flightless birds. Moreover, European colonization events could be also possible through Africa, which is consistent with the biogeographical relationship proposed for both continents during this period (Gheerbrant and Rage 2006; Ezcurra and Agnolin 2012; Novas et al. 2013). North American high colonization rates suggest that during the Upper Cretaceous probably existed different routes of biotic interchange from South America directly or across Africa-Europe. These patterns are consistent with diverse dispersal routes proposed for many dinosaur lineages with Laurasian origin that achieved to colonize South America and Antarctica (Benson et al. 2013; Novas et al. 2013). Finally, the high rates present in Zealand might indicate that an important crossing route towards Zealand was present during the Cretaceous as suggested by Sanmartín and Ronquist (2004).

During the middle Upper Cretaceous the Indian subcontinent, Madagascar and Australia showed an increase of their colonization rates (Fig.2, 3A). This is consistent with the drifting process that these landmasses experimented during the Gondwanan break up, with Madagascar and India diverging around 84 Ma and Australia beginning its separation of West Antarctica during the arise of Tasmanian Sea around 80 Ma (Sanmartín and Ronquist 2004). These processes probably promoted diverse events of vicariance in ancestral lineages and dispersal routes during the early drift process when still persisted a distance that would allow the colonization (Woodburne and Case 1996). Some authors have proposed a dispersal route between these landmasses via the Kerguelen plateau until Eocene times (Noonan and Chippindale 2006b; Chatterjee et al. 2013). Antarctica, South America and Asia presented a relative increase of colonization events around 80 Ma. Asian increases probably have relationship with the isolation that suffered Asiamerica respect to Euramerica during the Turonian sea level increase (Miller et al. 2003). This isolation would extend until the Santonian (Ezcurra and Agnolin 2012). During this period many North American faunal components invaded Asia due to the existence of a broad Bering route, which is consistent with many dinosaur biogeographic patterns (Serenio 1999). The South American and

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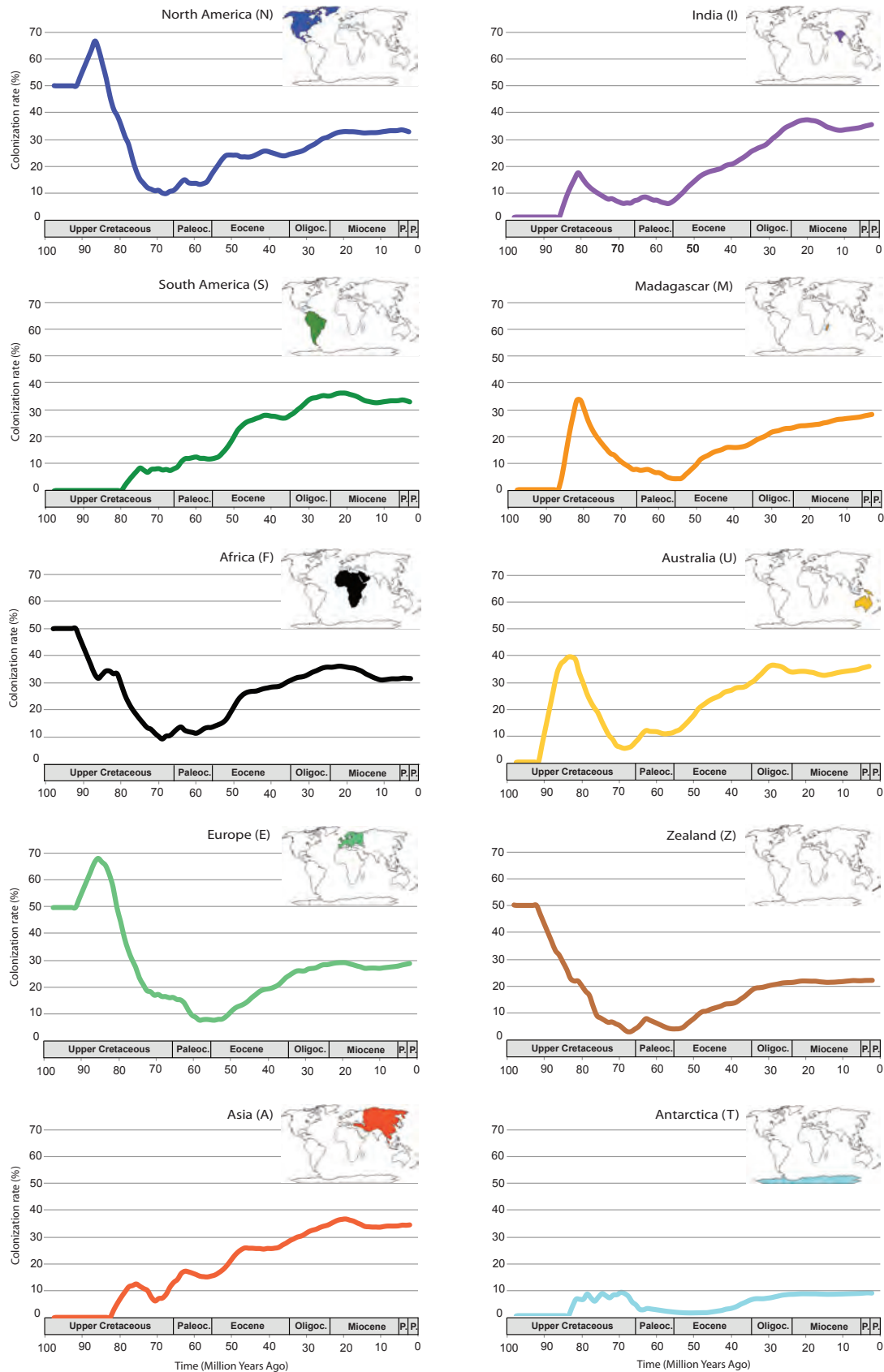


Figure 2. Neornithes colonization rates for in each continent along geologic time.

Antarctica colonizations may suggest an intense dynamics of dispersal events between the Gondwana continents caused by their relative nearness and the establishment of fluctuating land bridges that allowed biotic interchanges and vicariance processes (Sanmartín and Ronquist 2004; Turner 2004; Bocxlaer et al. 2006; Jacobs et al. 2011).

According to our results, around the late Upper Cretaceous all the continents present a substantial decreasing of their colonization rates (Fig. 2, 3A). This is possibly related to the confluence of diverse climate changes, geologic process and astronomical events that triggered the K/T event, in which many biotic groups became extinct (Archibald et al. 2010; Courtillot and Fluteau 2010; Schulte et al. 2010). The pattern obtained points to South America acting as a “cradle” for the early Neornithes birds, and supports the great influence of tectonic and climatic processes in the early evolution of modern birds. This “southern cradle” for Neornithes would implicate an important turnover in global avifaunas during the late Cretaceous and early Paleogene. According to fossil evidence, along the early and late Cretaceous, the terrestrial-arboreal niches were dominated by Enantiornithes birds (Sanz et al. 1996; Longrich 2009; O’Connor et al. 2011). Conversely, the ornithurine birds were prevalent in aquatic and semiaquatic ecosystems (Longrich 2009), which became abundant with the increase of sea levels during the Turonian (Miller et al. 2003). Enantiornithes bone histology suggest that ontogenic development in these birds was lower than in Ornithurinae (Chinsamy et al. 1995; Chinsamy and Elzanowski 2001). Ornithurine rapid development probably evolved as an adaptive answer to the high predation pressure that probably existed in relation to semiaquatic or ground nesting habits (Lima 2009). These traits and a faster ontogenetic growth probably allowed many ornithurine lineages to survive the late Cretaceous climate crisis, in which changed the plant physiognomy in forest environments where Enantiornithes lived. Likewise, many habitats in the southernmost latitudes of Gondwana probably acted as refugia for many ornithurine lineages, which remained isolated until they dispersed to lower latitudes during favourable periods (Schulte et al. 2010; Archibald et al. 2010). This evolutionary scenario was initially proposed for invertebrates (Zinsmeister and Feldmann 1984) and later extended to mammals (Reguero et al. 2002; Chimento et al. 2015).

Along the Paleocene and early Eocene our results suggest a generalised increase in colonization rates, which was more significant during the early Eocene (except in

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Antarctica) (Fig.2). These results have correspondence with the diversification observed in diverse terrestrial taxa and probably was related with the Paleocene-Eocene thermal maximum (Zachos et al. 2001), which would generate an important expansion of tropical environments polewards and implied the emergency of new niches due to use and availability of diverse food resources (Collinson and Hooker 2003; Jaramillo et al. 2010). Likewise, the presence of land bridges between North America and Europe, allow the colonization of many lineages (Brikiatis 2014), specially forest-dwelling birds (Fig.3A) (Mayr 2009). The novel ecological opportunities made possible the diversification of many frugivorous, insectivorous and even faunivorous taxa (Mayr 2009, 2011c). In this context, a new turnover is consistent with our results; during the early Paleogene Terrestrial, arboreal and actively flying avian lineages (i.e. Telluraves or Caprimulgiformes) occupied the empty terrestrial niches of extinct Enanthiornithes (Mayr 2009).

During the middle and late Eocene, there was a stabilization of colonization rates and a slight decrease around the Eocene-Oligocene boundary (Fig.2). These findings probably have relationship with climatic changes during the last phases of the Terminal Eocene Event 34 Ma (Zachos et al. 2001). Generalised global cooling could facilitate the establishment of a different biome configuration and the subsequent demise of previously widespread groups (Lindow and Dyke 2006). This is also evidenced for insect faunas which constitutes the main nourishment source of many bird species (Toussaint et al. 2012). This cooling trend probably presented major effects in North America, where semiopen deciduous woodlands replaced the ancient evergreen paratropical rainforest (Janis 1993; Fraser and Theodor 2013). These environmental changes affected probably the abundance of forest-arboreal birds from North America respect to Europe where the Tethys Sea acted like as climate moderator (Prothero and Berggren 1994; Akhmetiev et al. 2012). According to this, the European ecosystems would not have achieved the such cooling and drying as in North America (Prothero and Berggren 1994). This is consistent with the extinction of common early Eocene forest-dwelling birds in North America that persisted in Europe (i.e Coliiformes and Coraciiformes families) (Mayr 2009; Ksepka and Clarke 2010b; Ksepka and Clarke 2010c).

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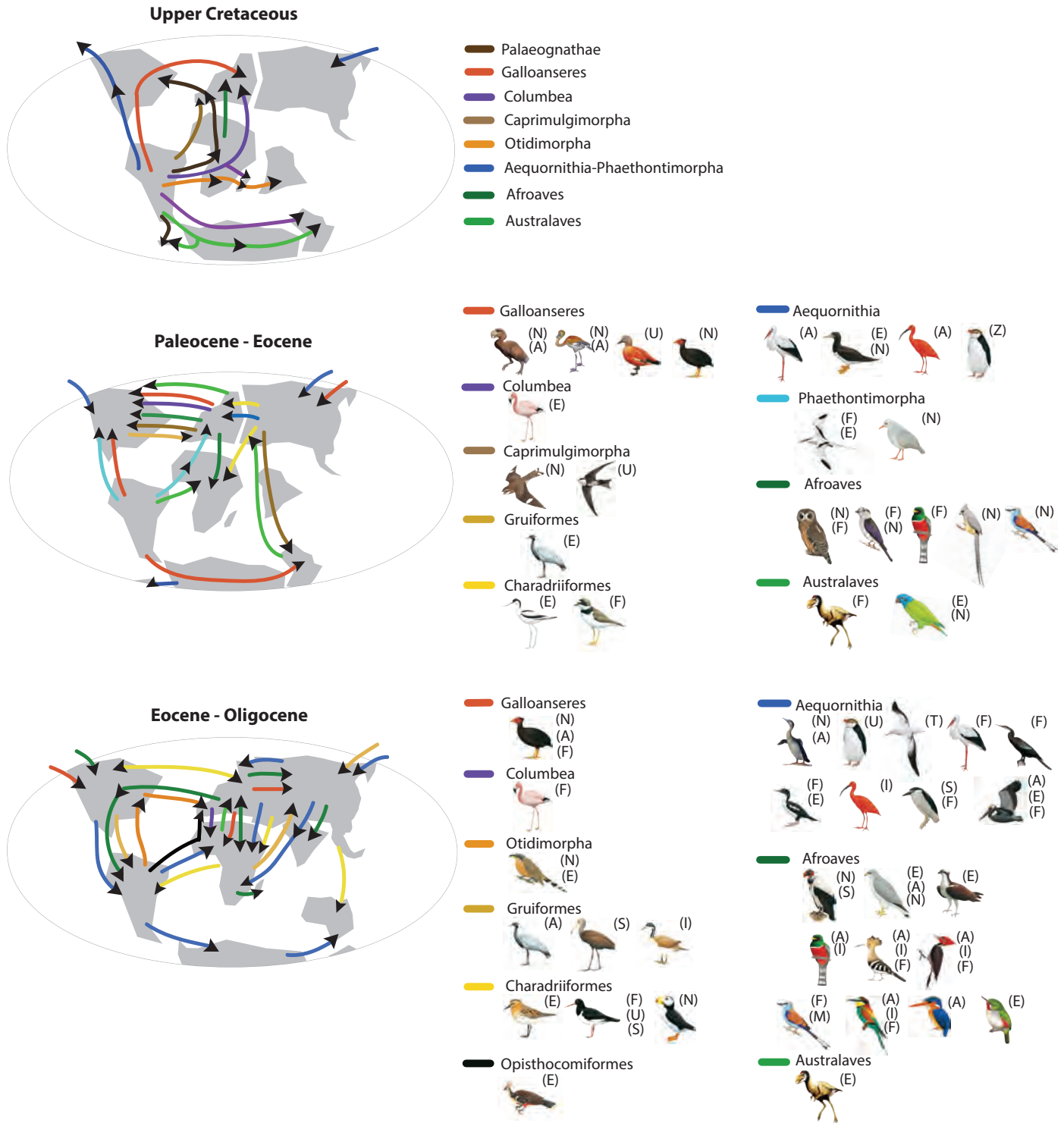


Figure 3A. Summary of paleobiogeographical reconstruction for dispersal main patterns during specific periods since Upper Cretaceous and during Paleogene, which were support by 1-0.5-0.1 Model, the fossil record and extant distribution of species. The bird figures indicate the closest clade implied in colonization event within the high-level clades according with the phylogenetic reconstruction of Figures 1A and 1B. The novel areas colonized are indicated with letter code (A= Asia; E= Europe; F= Africa; I= India; M= Madagascar; N= North America; S= South America; T= Antarctica; U= Australia; Z= Zealand).

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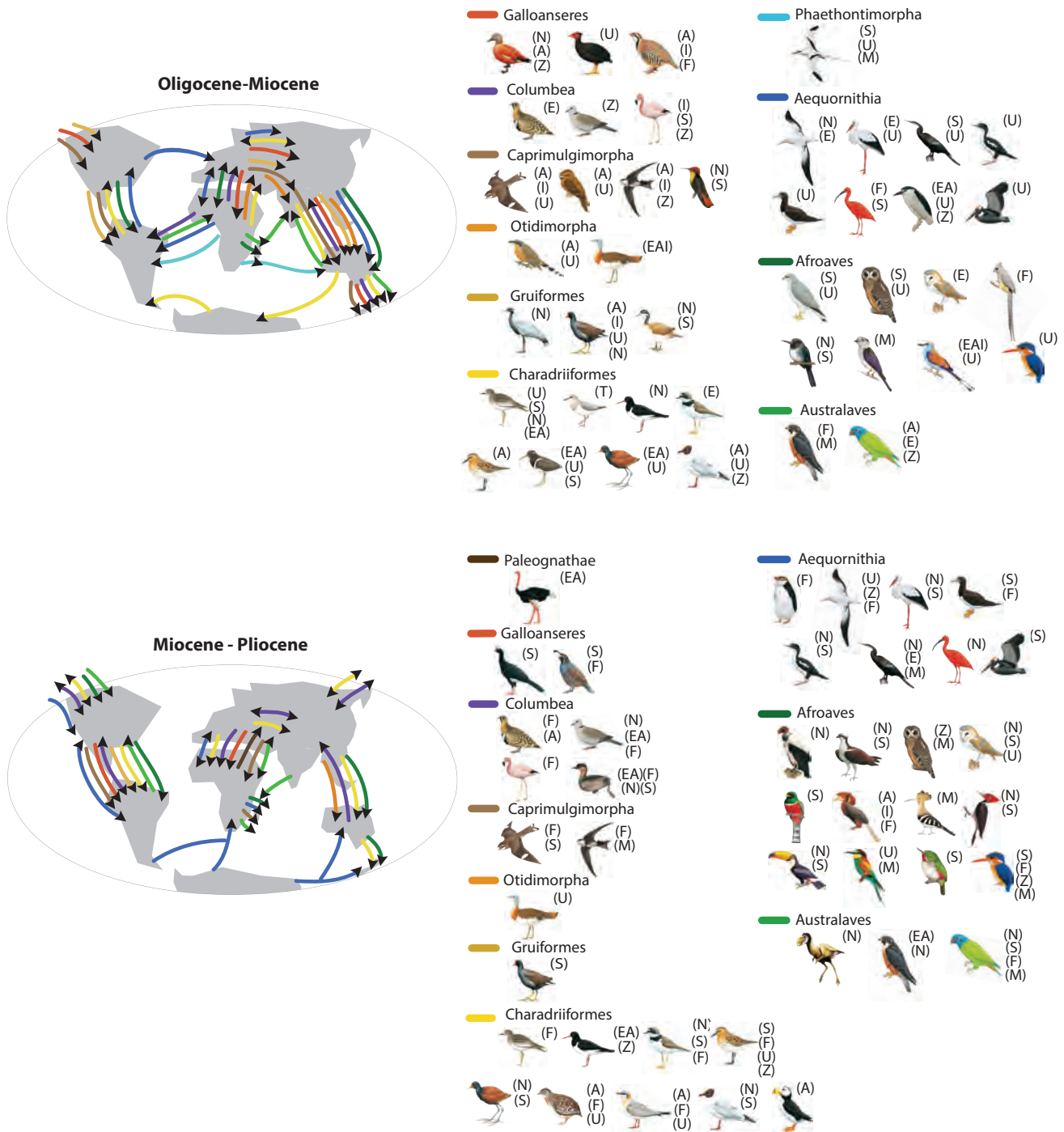


Figure 3B. Summary of paleobiogeographical reconstruction for dispersal main patterns during specific periods of Neogene, which were support by 1-0.5-0.1 Model, the fossil record and extant distribution of species. The bird figures indicate the closest clade implied in colonization event within the high-level clades according with the phylogenetic reconstruction of Figures 1A-B. The novel areas colonized are indicated with letter code (A= Asia; E= Europe; F= Africa; I= India; M= Madagascar; N= North America; S= South America; T= Antarctica; U= Australia; Z= Zealand).

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On the other hand, our results suggest that probably diverse lineages dispersed from Europe to Asia (i.e. Eogruidae, Protostrigidae, Strigidae, Meropidae, Upupidae and Trogonidae)(Fig.3A-3B). This process is agreement with The Grande Coupure (Stehlin 1909; Costa et al. 2011) studied in mammals faunas, which allowed the direct entry in Europe of diverse Asian lineages (Prothero and Berggren 1994). These interchange probably increased predation ecological interactions causing the extinction of lineages with low flying capacity such galliforms Paraortygidae and Quercymegapodidae (Mayr 2011c, 2009). The observed tendencies in South America and Antarctica showed an increase of colonization rates during the early Oligocene, this pattern could be related with the cooling process due to the opening of Drake Passage, which generated a new climate regime southwards associated with the circunantarctic ocean currents promoting early icesheets in Antarctica (Francis et al. 2008). The isolation of Antarctica probably promoted the adaptation to cold conditions and allowed the colonization and diversification of diverse lineages of Sphenisciformes and Procellariiformes (Clarke et al. 2007; Ksepka and Clarke 2010a).

The late Oligocene and early Miocene reported the maximum value for colonization rates during the Cenozoic in all continents (Fig.3A-3B). During the Oligocene, the Earth ecosystems experimented important changes through major climate change (Zachos et al. 2001). The cold and arid conditions would facilitate the development of semiopen biomes dominated by C3 grassy species and the evolution of C4 species that spread later across the Late Miocene and Pliocene (Edwards et al. 2010) due to the gradual fragmentation of forest environments restricted to the wet ecotones and the equatorial zones (Woodward et al. 2004). The earlier drier conditions promoted plant adaptations in subtropical forests that allowed a broad expansion during the maximal thermal period between Late Oligocene Warming Event and Miocene Maximum Climate Optimum (Zachos et al. 2001). Under this ecological context, many new lineages adapted to seasonal and dry conditions were able to spread across the continents (Mayr 2011c). Moreover, important crossing routes were established between Africa and Eurasia that made possible the biotic interchange between the continents in middle Miocene times (Pickford and Morales 1994; van der Made 1999; Sen 2013). During this period the avifauna in Europe and Africa presented high similarity, many species of African lineages adapted to dry, open and semiopen environments (Otidiformes and Musophagiformes) and even expanded their

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distribution toward similar environments in Europe and Asia (Otididae)(Sánchez Marco 1990; Mlíkovský 2002). Likewise, terrestrial lineages such ostriches (Struthionidae) lineage colonized Europe (Mlíkovský 2002; Mayr 2011c) and Asia (Hou et al. 2005) during the Miocene in line with mammals interchanges during the *Tethytragus* or *Gazella* event (van der Made 1999). From Europe, lineages such Bucerotidae colonized Africa and subsequently Asia during the middle and late Miocene. The intense cooling and aridity process during the late Miocene and Pliocene (van Dam 2006) generated the appearance of a marked seasonal regime in the Northern Hemisphere. This scenario probably implied the retraction of geographical distribution for lineages adapted to tropical conditions in the northern latitudes (Mayr 2011c), which remained in the tropical biomes that persisted in Africa as evidenced Coliidae, Indicatoridae, Struthionidae, and Psittacidae. Probably the development of migratory behaviour in lineages such Meropidae, Coraciidae, Otididae and Upupidae allowed them cope these emerging climatic conditions and conserve their broad distribution in the Old World (Rolland et al. 2014; Pelegrin et al. 2015).

In a parallel process respect to Europe and Africa, diverse North American lineages, many of them coming from Asia using the Bering Land Bridge (Sanmartín et al. 2001) (Fig.3A, 3B) (i.e Gruidae and Rallidae), or with African and European origin through the North Atlantic land bridges such as diverse groups of Coraciformes, Alcediniformes y Piciformes (Sanmartín et al. 2001; Tiffney 2008), were adapted to inhabit warm and dry conditions during the early and middle Miocene. Without adaptations to cope winter conditions, these birds would disperse southward to Central America and later entered in South America. The proximity between North America and South America might generate diverse dispersal events for lineages with high-flying capacity until the terrestrial contact during the Miocene-Pliocene (Montes et al. 2015; Hoorn and Flantua 2015) (Fig.3B). This biogeographical frame explains presence and diversification of warm adapted lineages such as Trochilidae (McGuire et al. 2014), Trogonidae (Dacosta and Klicka 2008), Todidae (Overton and Rhoads 2004) and Ramphastidae (Lutz et al. 2013) in Neotropics since late Miocene until Pleistocene.

Our results suggest an intense increase of colonizations in Australia during the Early Miocene (Fig.3B). In this period, Australia collided with Asia and this process triggered the formation of the Wallacea archipelago during middle-late Miocene (Hall 2009). Which would be crucial in different dispersal opportunities between Asia and

Australia. Wallacea would have worked as “stepping stones” promoting a crossing route as well as an important scenario for speciation in the different islands (Condamine et al. 2013; Moyle et al. 2009). Our findings are consistent with models proposed for Megapodiidae biogeography (Harris et al. 2014) and colonization processes reported for mammals (Rowe et al. 2008).

In a broad view, the analysis of biogeographic patterns in both hemispheres suggested a substantial influence of flight capacity developed by early modern bird ancestors (Mayr 2009), which allowed diverse colonizations achieved some of them broad distributions (i.e. Cursoriomorphae). Their role is evidenced also in the continuous colonization rates in the India, Zealand or Madagascar, which have been isolated during long periods. Nevertheless, southern hemisphere patterns show that the distributions of many bird taxa are also explained by vicariance events, in line with the Gondwana break up as previously proposed for birds and other animal groups (Cracraft 2001; Ericson et al. 2002; Sanmartín and Ronquist 2004; Bocxlaer et al. 2006; Yoder and Nowak 2006; Noonan and Chippindale 2006a).

3.5.11. Aquatic birds: paleobiogeographic patterns and evolutionary processes

The results suggest that the aquatic lineages that achieved a wide distribution during their early evolution would reach a constant permanency avoiding the extinction (De Queiroz 2005). The colonization of islands, where the predation pressures are lesser, the development of a broad spectrum of diet, as well as the colonial mating strategy and the migratory behaviour are important features that probably contributed to ecological success of many aquatic groups (Jetz et al. 2008; García-Peña et al. 2009; Davies et al. 2010). Likewise, the intense climate changes transformed the sea currents, their productivity, and equally the availability of adaptive zones. These variations would trigger that some clades were able to survive better than others (Walls et al. 2005; Dobrovolski et al. 2012). According to this, the extinction of lineages such Plotopteridae coincident with the Eocene-Oligocene climate transition and the radiation of Pan-alcidae could suggest a scenario of ecological turnover (Dyke et al. 2011; Smith and Clarke 2014). In the same way, the decrease in Phaethontiformes lineages probably had a relationship with the diversification of marine Lari lineages. Also, specialist lineages such Diomedeoidea, Prophaethontidae and Laricolidae restricted to Tethys and Paratethys area (Mlíkovský 2009; Elzanowski et

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al. 2012; De Pietri et al. 2011) probably were affected by the environmental changes in these seas during Oligocene and Miocene (Rögl 1999)(Fig. 3A, 3B). Other seabirds would be affected by the evolution of Pinniped mammals during Late Oligocene (Churchill et al. 2015; Kelley and Pyenson 2015), altering the ecological scenario. Conversely, other birds such as Anhingidae would increase their diversity during the middle and late Miocene (Cenizo and Agnolín 2010), probably influenced by the expansion towards tropical conditions during the Mid-Miocene climate optimum (Zachos et al. 2001). Finally, it's difficult to establish whether there is a causal relationship between the diversification of some aquatic lineages and the extinction of others. However our reconstruction may constitute a first approach to propose a general frame for hypothetical phases of turnover in seabird lineages in relation with climate and geological changes, which could be improved in the future with new fossil findings.

Overall, our study supports that the Africa-Europe connection constitutes an important route of biotic interchange in the avian history, which is consistent with the model proposed by Ezcurra and Agnolín (2012). Along the geological time, diverse abiotic processes altered and transform the ecosystems worldwide. According to this, our findings propose an outstanding connection between these processes and the colonization patterns in diverse bird clades, which allowed the subsequent diversification and occupancy of novel adaptive zones. In this way, the development of some traits (i.e. diet, physiology, tree-dwelling, migration, etc) enabled certain groups to survive and cope diverse environmental changes. Likewise, many extinction events registered in the avian fossil record showed consistency with our results. Finally, we can conclude that geologic processes and the climate changes have been the main factors affecting deep-time biogeographic patterns in birds.

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3.8. Appendix



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Appendix 3.8.1. Table S1. Paleontological and geographical information of extinct families included in phylogenetic tree. **FAD:** FIRST APARITION DATA; **LAD:** LAST APARITION DATA; **Geog. Area:** Geographic Area. **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Clade	Geog. Area	Fossil Age (M.a) FAD	Fossil Age (M.a) LAD	References
Palaeotididae +	(E)	47.80	38.00	(Houde and Haubold 1987; Mlíkovský 2002; Mayr 2009a)
Aepyornithidae +	(F) (M)	0.01	0.01	(Burney et al. 2004; Mayr 2009a)
Dinornithiformes +	(Z)	19.00	16.00	(Worthy et al. 2007; Bunce et al. 2009; Tennyson et al. 2010)
Lithornithidae +	(N) (E)	62.00	47.80	(Houde 1988; Kristoffersen 1999; Leonard et al. 2005; Mayr 2009b, a; Stidham et al. 2014)
Dromornithidae +	(U)	28.10	2.58	(Vickers-Rich 1991; Murray and Megirian 1998; Mayr 2009a; Park and Fitzgerald 2012; Olson 2005)
Gastornithidae +	(N) (E) (A)	59.20	47.80	(Olson 1985; Mlíkovský 2002; Mayr 2005a; Lindow and Dyke 2006; Mayr 2009a; Angst et al. 2014)
Pelagornithidae +	(N) (S) (F) (E) (A) (T)	59.20	2.58	(Bourdon et al. 2010; Mayr and Rubilar-Rogers 2010; Boessenecker and Smit 2011; Mayr and Zvonok 2011; Mayr 2011; Ksepka 2014)
Presbyornithidae +	(N) (S) (A)	72.10	33.90	(Livezey 1997; Ericson 2000; Kurochkin et al. 2002; Lindow and Dyke 2006; Mayr 2009a; Elzanowski and Stidham 2010)
Gallinuloididae +	(N) (E)	56.00	47.80	(Mayr and Weidig 2004; Weidig 2003; Lindow and Dyke 2006; Mayr 2009a, 2014b)
Paraortygidae +	(E)	38.00	23.03	(Mourer-Chauviré 1992; Mayr 2009a; Mourer-Chauviré et al.

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				2011)
Quercymegapodiidae +	(N) (S) (E)	69.20	20.44	(Alvarenga 1995; Mlíkovský 2002; Mayr 2009a; Mourer-Chauviré et al. 2011)
Archaeotrogonidae +	(E)	56.00	23.03	(Mlíkovský 2002; Mayr 2005a, 2009a)
Fluvioviridavidae +	(N) (E)	56.00	47.80	(Mayr 2009a; Nesbitt et al. 2011)
Eocypselidae +	(E)	56.00	47.80	(Mayr 2003; Mayr 2009a, 2010, 2014b)
Prophaethontidae +	(N) (F) (E) (A)	66.00	41.30	(Bourdon et al. 2005; Mayr 2005a; Mlíkovský 2002; Mayr 2009a; Mlíkovský 2009)
Palaelodidae +	(N) (S) (E) (F) (U) (Z)	56.00	2.58	(Mlíkovský 2002; Mayr 2004, 2005a, 2009a; Worthy et al. 2010; Mayr 2014a)
Onychopterygidae +	(S)	47.80	41.30	(Cracraft 1971; Mayr 2009a; Tambussi and Degrange 2013)
Eogruidae +	(E) (A)	56.00	3.60	(Cracraft 1969; Clarke et al. 2005; Mayr 2009a, 2014b)
Geranoididae +	(N)	56.00	47.80	(Cracraft 1969; Mayr 2009a)
Messelornithidae +	(N) (E)	66.00	47.80	(Lindow and Dyke 2006; Mayr 2009a; Weidig 2010)
Aptornithidae +	(Z)	20.44	2.58	(Worthy et al. 2007; Worthy et al. 2011)
Plotopteridae +	(N) (A)	38.00	33.90	(Warheit 1992; Olson and Hasegawa 1996; Mayr 2005b, 2009a)
Diomedeooididae +	(E) (A)	33.90	28.10	(Mlíkovský 2002; Mayr 2005a, 2009a; Mlíkovský 2009)
Protoplotidae +	(A)	59.20	47.80	(van Tets et al. 1989; Mayr 2009a)
Laricolidae +	(E)	29.10	28.10	(Mlíkovský 2002; De Pietri et al. 2011; Smith 2015)
Teratornithidae +	(S)	28.10	0.01	(Campbell and Tonni 1980; Olson 1985; Mayr 2009a; Vizcaíno and Fariña 1999; Tambussi and

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Degrange 2013)				
Sophiornithidae +	(E) (A)	59.20	23.03	(Mayr 2009a; Kurochkin and Dyke 2012)
Ogygoptyngidae +	(N)	59.20	56.00	(Mayr 2009a; Kurochkin and Dyke 2012)
Protostrigidae +	(N) (E)	56.00	28.10	(Mayr 2009a; Kurochkin and Dyke 2012)
Panleptosomidae +	(N) (E)	56.00	41.30	(Weidig 2006; Mayr 2008, 2009a; Weidig 2010; Mayr 2014b)
Messelirrisoridae +	(E)	56.00	47.80	(Mlíkovský 2002; Mayr 2006, 2009a, 2014b)
Primobucconidae +	(N) (E)	56.00	47.80	(Mayr 2005a; Clarke et al. 2009; Mayr 2009a; Ksepka and Clarke 2010a; Weidig 2010; Mayr 2014b)
Eocoraciidae +	(E)	56.00	47.80	(Mayr and Mourer-Chauviré 2000; Mayr 2005a; Clarke et al. 2009; Mayr 2009a; Ksepka and Clarke 2010a)
Geranopteridae +	(E)	38.00	33.90	(Mayr and Mourer-Chauviré 2000; Mayr 2005a; Clarke et al. 2009; Mayr 2009a)
Sylphornithidae +	(E)	41.30	28.00	(Mlíkovský 2002; Mayr 2005a, 2009a)
Gracilitarsidae +	(E)	47.80	38.00	(Mayr 2001; Mlíkovský 2002; Mayr 2005a, 2009a)
Picavidae +	(E)	33.90	28.10	(Mayr and Gregorová 2012)
Sandcoleidae +	(N) (E)	56.00	41.30	(Mayr 2005a; Lindow and Dyke 2006; Zelenkov and Dyke 2008; Mayr 2009a; Ksepka and Clarke 2010b; Mayr 2014b)
Chascacocoliidae +	(N) (E)	56.00	47.00	(Mayr 2009a, 2013; Zelenkov and Dyke 2008; Ksepka and Clarke 2010b)
Ameginornithidae +	(E) (F)	47.80	33.0	(Peters 2007; Mayr 2009a; Stidham and Smith 2015)
Phorusrhascidae +	(S)(E)(N)	59.20	1.81	(Alvarenga and Höfling 2003; Mayr

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2009a; Tambussi 2011; Tambussi and Degrange 2013)				
Idiornithidae +	(E)	47.80	23.03	(Alvarenga and Höfling 2003; Mayr 2005a, 2009a)
Halcyornithidae +	(N) (E)	56.00	47.80	(Mayr 2009a; Ksepka et al. 2011; Ksepka and Clarke 2012; Mayr 2014b)
Quercypsittidae +	(E) (I)	56.00	47.80	(Mayr 2009a; Mayr et al. 2010; Ksepka and Clarke 2012)
Zygodactylidae +	(E)	56.00	23.00	(Mayr 2009a; Weidig 2010; Mayr 2014b)

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Appendix 3.8.2. Table S2. Paleontological and geographical information for extinct relatives of recent families included in phylogenetic tree. **FAD:** FIRST APARITION DATA; **LAD** LAST APARITION DATA; **AO:** ANCESTRAL OCCUPATION; **Geog. Area:** Geographic Area. **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand; **(*)** Various species for the genera.

Clade	Fossil taxon	Geographic Area	Fossil Age (M.a) FAD	Fossil Age (M.a) LAD	References
Struthionidae	<i>Struthio coppensi</i>	(F)	23.30	20.44	(Mourer-Chauviré et al. 1996; Pickford 2004; Mayr 2009)
Rheidae	Rheidae indet.	(S)	61.60	59.20	(Alvarenga 1983; Tambussi 1995; Mayr 2009)
Tinamidae	<i>Crypturellus reai</i>	(S)	20.44	15.97	(Chandler 2012; Bertelli et al. 2014)
Dromaiidae	<i>Emuarius gidju</i>	(U)	28.10	23.30	(Boles 1992; Mayr 2009; Worthy et al. 2014)
Casuariidae	<i>Casuarus</i> sp.	(U)	3.60	2.58	(Hoch and Holm 1986; Alroy 2014)
Apterygidae	<i>Proapteryx micromeros</i>	(Z)	20.44	15.97	(Worthy et al. 2013)
Anseranatidae AO	<i>Anatalavis oxfordi</i>	(N) (E)	69.20	65.00	(Olson 1999a; Mayr 2014c)
Anseranatidae	<i>Eoanseranas handae</i>	(U)	28.10	20.44	(Worthy and Scanlon 2009)
Anhimidae AO	Anhimidae indet.	(U)	56.00	47.80	(Elzanowski and Boles 2012)
Anhimidae	<i>Chaunoides antiquus</i> <i>Loxornis clivus</i>	(S)	28.10	20.44	(Alvarenga 1999; Mayr 2009)
Anatoidea AO	<i>Vegavis iaai</i>	(T)	72.10	66.00	(Clarke et al. 2005)
Anatidae AO	<i>Romainvillia stehlini</i>	(E)	38.00	33.90	(Mayr 2009; Mayr and De Pietri 2013)
Anatidae	<i>Mionetta blanchardi</i> <i>Pinpanetta</i> sp. (3) <i>Australotadorna alecwilsoni</i> <i>Teleornis impressus</i>	(E) (U) (U) (S)	33.90	28.10	(Mayr 2008b, 2009)
Galliformes AO	Galliformes indet	(A)	59.20	47.80	(Hwang et al. 2010)
Megapodiidae	<i>Ngawupodius minya</i>	(U)	28.10	23.03	(Boles and Ivison 1999; Mayr 2009)
Cracidae AO	<i>Procrax brevipes</i>	(N)	38.00	33.90	(Mayr and Weidig 2004; Mayr 2009)
Cracidae	<i>Palaeonossax senectus</i>	(N)	33.90	28.10	(Wetmore 1956; Mayr 2009)

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Numididae AO	<i>Telecrex grangeri</i>	(A)	38.00	33.90	(Olson 1974; Mayr 2009)
Numididae	<i>Numida</i> sp.	(F)	3.60	2.58	(Alroy 2014)
Phasianidae AO	<i>Palaeortyx gallica</i>	(E)	28.10	23.03	(Mourer-Chauviré 1992; Mayr et al. 2006; Mayr 2009)
Phasianidae	<i>Schaubortyx keltica</i>	(E)	29.00	27.50	(Mayr et al. 2006; Mayr 2009)
Odontophoridae	<i>Nanortyx inexpectatus</i>	(N)	38.00	33.90	(Mayr 2009)
Eurypygidae AO	<i>Eoeurypyga olsoni</i>	(N)	53.50	48.50	(Weidig 2003; Mayr 2009)
Rhynchoetidae	<i>Rhynchoetos orarius</i>	(U)	0.01	0.00	(Del Hoyo et al. 1996; Balouet and Olson 1989)
Podargidae AO	<i>Masillapodargus longipes</i>	(E)	41.30	38.00	(Mayr 2001; Mayr 2009; Nesbitt et al. 2011; Ksepka et al. 2013)
Steatornithidae AO	<i>Prefica nivea</i>	(N)	56.00	47.80	(Mayr 1999; Mayr 2001; Mayr 2009; Nesbitt et al. 2011; Ksepka et al. 2013)
	<i>Euronyctibius kurochkini</i>	(E)	47.80	38.00	(Mayr 1999, 2009; Ksepka et al. 2013; Mayr 2014c)
Nyctibiidae AO	<i>Paraprefica kelleri</i>	(E)	47.80	38.00	(Olson 1999b; Mayr 2009)
Caprimulgidae AO	Caprimulgidae indet.	(N)	56.00	47.20	(Mourer-Chauviré 1988, 1989; Mayr 2009)
Caprimulgidae	<i>Ventivorus ragei</i>	(E)	40.40	37.20	(Worthy et al. 2007; Alroy 2014)
Aegothelidae	<i>Aegotheles</i> sp.	(U)	19.00	16.00	(Mayr 2005; Mayr 2009; Ksepka et al. 2013)
Trochilidae AO	<i>Parargornis messelensis</i>	(E)	56.00	47.80	(Mayr 2009; Mayr and Micklich 2010; Ksepka et al. 2013)
Trochilidae	<i>Eurotrochilus inexpectatus</i>	(E)	33.90	28.10	(Mayr and Peters 1999; Mayr 2009; Ksepka et al. 2013)
Apodidae AO	<i>Collocalia buday</i>	(E)	56.00	33.90	(Bourdon et al. 2008)
Phaethontidae	<i>Phaethusavis pelagicus</i>	(F)	56.00	47.80	(Olson and Feduccia 1980; Ericson 1999; Mayr 2004, 2009, 2014a)
Phoenicopteriformes AO	<i>Juncitarsus merelli</i>	(E)	56.00	47.80	

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Phoenicopteridae AO	<i>Phoeniconotius eyrensis</i>	(U)	28.10	23.03	(Miller 1963; Mayr 2009, 2014a)
Phoenicopteridae	<i>Phoenicopterus</i> sp.	(E)	28.10	23.03	(Mayr 2009, 2014a)
Podicipediformes AO	Podicipediformes indet.	(A) (U)	28.10	20.44	(Kurochkin 1976; Vickers-Rich 1991)
Podicipedidae	<i>Miobaptus walteri</i>	(E)	20.44	15.97	(Švec 1982, 1984; Mayr 2004, 2009)
Pteroclididae AO	<i>Archaeoganga pinguis</i>	(E)	28.10	23.03	(Mourer-Chauviré 1993; Mlíkovský 2002; Mayr 2009)
Pteroclididae	<i>Leptoganga sepultus</i>	(E)	24.60	24.60	(Mourer-Chauviré 1993; Mlíkovský 2002; Mayr 2009, 2014c)
Columbidae AO	Columbidae indet.	(U)	28.10	23.00	(Vickers-Rich 1991; Worthly et al. 2007)
Opisthocomidae AO	<i>Protazin parisiensis</i>	(E)	34.00	33.00	(Mayr and De Pietri 2014; Mayr 2014c)
Opisthocomidae	<i>Hoazinavis lacustris</i>	(S)	28.00	20.44	(Mayr et al. 2011b; Mayr and De Pietri 2014)
Aramidae AO	<i>Badistornis aramus</i>	(N)	33.90	28.10	(Chandler and Wall 2001; Mayr 2009)
Aramidae	<i>Loncornis erectus</i>	(S)	28.00	0.00	(Agnolin 2004; Mayr 2009)
Gruidae AO	<i>Palaeogrus princeps</i> <i>Eobalearica tugarinovi</i>	(E) (A)	47.80	41.30	(Mlíkovský 2002; Mayr 2009)
Gruidae	Gruidae indet.	(N)	33.90	11.62	(Olson 1985; Mayr 2009)
Rallidae AO	<i>Songzia heidangkouensis</i>	(A)	56.00	47.80	(Hou 2003)
Rallidae	<i>Belgirallus oligocaenus</i> Rallidae indet.	(E) (F)	33.9	32.40	(Mayr and Smith 2001; Mayr 2009)
Heliornithidae AO	<i>Heliornis</i> sp.	(N)	15.97	11.62	(Olson 2003; Louchart et al. 2005)
Otididae AO	Otididae indet.	(F)	13.82	11.62	(Alroy 2014)
Otididae	<i>Otis bessarabensis</i>	(E)	13.10	11.20	(Sanchez Marco 1990; Mlíkovský 2002)
Cuculidae AO	<i>Eutreptodactylus itaboraiensis</i>	(S)	59.20	56.00	(Mayr et al. 2011a; Tambussi and Degrange 2013)
Cuculidae	<i>Chambicuculus pusillus</i>	(F)	47.00	41.30	(Mourer-Chauviré et al. 2013b; Mayr 2014c)
Musophagiformes AO	Musophagiformes indet.	(F)	33.90	28.10	(Rasmussen et al. 1987; Mayr 2009)

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Gaviiformes AO	<i>Polarornis gregorii</i>	(T)	72.10	66.00	(Chatterjee 2002; Tambussi and Acosta Hospitaleche 2007; Mayr 2014c)
Gaviidae	<i>Colymbiculus udovichenkoi</i>	(E)	47.80	38.00	(Mayr and Zvonok 2011; Mayr et al. 2013; Mayr 2014c)
Sphenisciformes AO	<i>Waimanu manningi</i>	(Z)	61.00	59.00	(Ksepka et al. 2006; Slack et al. 2006; Clarke et al. 2007; Mayr 2009; Ksepka and Clarke 2010a; Mayr 2014c)
Spheniscidae	<i>Delphinornis larseni</i>	(T)	47.8	33.9	(Clarke et al. 2007; Mayr 2009; Ksepka and Clarke 2010a)
	<i>Perudyptes devriesi</i>	(S)		41.3	
Procellariiformes AO	<i>Lonchodytes pterygius</i>	(N)	72.10	65.00	(Hope 2002; Mayr 2009)
Hydrobatidae	<i>Oceanodroma hubbsi</i>	(N)	11.62	7.24	(Alroy 2014)
Diomedidae	<i>Tydea septentrionalis</i>	(E)	33.90	28.10	(Mayr and Smith 2012)
Procellariidae AO	<i>Argyrodypes microtarsus</i>	(S)	38.00	28.10	(Agnolin 2004; Mayr 2009; Tambussi and Degrange 2013)
Pelecanoididae	<i>Pelecanoides miokuaka</i>	(Z)	20.44	15.97	(Worthy et al. 2007)
Ciconiidae AO	<i>Eociconia sangequanensis</i>	(A)	47.80	38.00	(Hou 2003; Mayr 2009)
Ciconiidae	<i>Palaeoephippiorhynchus dietric</i>	(F)	33.9	28.10	(Rasmussen et al. 1987; Olson 1985; Mayr 2009, 2014c)
Fregatidae AO	<i>Limnofregata azygosternon</i>	(N)	56.00	47.80	(Olson and Matsouka 2005; Mayr 2009, 2014c)
Sulidae AO	<i>Masillastega rectirostris</i>	(E)	48.60	46.00	(Mayr 2002b, 2009, 2014c)
Sulidae	<i>Eostega lebedinskyi</i>	(E)	37.20	33.90	(Mlíkovský 2002, 2009)
Anhingiidae AO	<i>Liptornis hesternus</i>	(S)	15.97	13.82	(Tambussi 2011; Tambussi and Degrange 2013)
Phalacrocoracidae AO	Phalacrocoracidae indet.	(N)	72.10	66.00	(Hope 2002; Mayr 2009)
Phalacrocoracidae	<i>Piscator tenuirostris</i>	(E)	38.0	33.90	(Mayr 2009, 2014c)
Pelecaniformes AO	<i>Torotix clemensi</i>	(N)	69.20	66.00	(Hope 2002; Mayr 2009)
Ardeidae AO	<i>Calcardea junnei</i>	(N)	56.00	47.80	(Sallaberry et al.

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					2010)
Ardeidae	<i>Gnotornis aramiellus</i>	(N)	33.90	28.1	(Olson 1985; Mayr 2009, 2014c)
	<i>Nycticorax</i> sp.	(E)			
Threskiornithidae	<i>Rhynchaetes messelensis</i>	(E)	56.00	41.30	(Mayr 2002a, 2014c)
AO					
Pelecanidae	<i>Pelecanus</i> sp.	(E)	33.90	0.00	(Louchart et al. 2010; Altamirano-Sierra 2013; Mayr 2014c)
Balaenicipitidae	<i>Goliathia andrewsi</i>	(F)	38.00	28.10	(Olson 1985; Mayr 2009, 2014c)
Scopidae	<i>Scopus xenops</i>	(F)	5.33	3.60	(Olson 1984, 1985; Alroy 2014)
Burhinidae AO	<i>Wilaru tedford</i>	(U)	24.00	26.00	(Boles et al. 2013)
Burhinidae	<i>Genocrassum bransatensis</i>	(E)	23.4	23.03	(De Pietri and Scofield 2013; Smith 2015)
Recurvirostridae	<i>Recurvirostra sanctaeneboulae</i>	(E)	56.00	47.80	(Mourer-Chauviré 1978; Mlíkovský 2002; Mayr 2009)
AO					
Haematopodidae	<i>Haematopodidae</i> indet.	(E)	22.50	20.44	(De Pietri et al. 2013)
AO					
Haematopodidae	<i>Haematopodus</i> sp.	(N)	5.33	3.60	(De Pietri et al. 2013)
Charadriidae	<i>Jiliniornis huadianensis</i>	(A)	47.80	38.00	(Hou and Ericson 2002; Smith 2015)
AO					
Scolopacidae	<i>Paractitis bardi</i>	(N)	37.20	33.90	(Olson 1999b; Mayr 2009)
AO					
Scolopacidae	<i>Scolopacidae</i> indet.	(E)	33.9	0.00	(Roux 2002; Mayr 2009)
Rostratulidae	<i>Rostratula pulia</i>	(E)	17.20	16.40	(Mlíkovský 2002)
AO					
Jacanidae AO	<i>Nupharanassa totularia</i>	(F)	38.00	28.00	(Rasmussen et al. 1987; Mayr 2009; Smith 2015)
Pedionomidae	<i>Oligonomis milleri</i>	(U)	26.00	24.00	(De Pietri et al. 2014)
Turnicidae AO	<i>Turnipax oechslerorum</i>	(E)	34.90	28.10	(Mayr and Knopf 2007; Smith 2015)
Glareolidae AO	<i>Boutersemia</i> sp.	(E)	33.90	28.10	(Mayr and Smith 2001; De Pietri et al. 2011a)
Glareolidae	<i>Mioglareola gregaria</i>	(E)	23.03	15.97	(De Pietri et al. 2011a)
	<i>Paractiornis</i> sp.	(N)			
Panalcidae	<i>Panalcidae</i> incertae sedis	(N)	38.00	33.90	(Chandler and Parmley 2002; Wijnker and Olson 2010)

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					2009; Smith 2011; Smith 2015)
Alcidae	<i>Miocepphus bohaski</i>	(N)	20.43	15.97	(Wijnker and Olson 2009; Smith and Clarke 2014; Smith 2015)
Stercorariidae	<i>Stercorarius</i> sp.	(N)	5.33	3.60	(Olson and Rasmussen 2001)
Laridae	<i>Larus dolnicensis</i>	(E)	17.10	16.40	(Mlíkovský 2002; De Pietri et al. 2011a)
Cathartoidea AO	<i>Diatropornis ellioti</i>	(E)	41.30	33.90	(Mourer-Chauviré 2002, 2006; Mayr 2009, 2011, 2014c)
Cathartidae	<i>Phasmagyps patritus</i>	(N)	38	33.90	(Mayr 2009, 2011, 2014c)
Sagittariidae AO	<i>Pelargopappus schlosseri</i>	(E)	33.90	23.03	(Mourer-Chauviré and Cheneval 1983; Mayr 2009)
Accipitridae AO	<i>Milvodes kempí</i> <i>Accipitridae</i> indet.	(E) (F)	38.00	33.90	(Mayr 2009, 2014c)
Accipitridae	<i>Buteo</i> sp.	(N) (A)	33.90	0.00	(Kurochkin 1976; Mayr 2009)
Pandionidae AO	Pandionidae indet.	(E)(F)	38.00	28.10	(Mayr 2009, 2014c)
Pandionidae	<i>Pandion</i> sp.	(N)	15.97	0.00	(Olson 1985; Mayr 2009)
Strigidae	<i>Myoglaux poirrieri</i>	(E)	21.70	17.50	(Mlíkovský 2002; Kurochkin and Dyke 2012)
Tytonidae AO	<i>Necrobyas arvernensis</i> <i>Selenornis henrici</i>	(E)	40.00	24.00	(Mlíkovský 2002; Mayr 2009; Kurochkin and Dyke 2012)
Tytonidae	<i>Basityto rummeli</i>	(E)	21.70	17.20	(Mlíkovský 2002; Kurochkin and Dyke 2012)
Leptosomatidae AO	<i>Plesiocathartes</i> sp.	(N) (E)	56.00	41.30	(Mayr 2008a, 2009, 2014c)
Trogoniformes AO	<i>Septentrogon madseni</i>	(E)	54.50	54.00	(Lindow and Dyke 2006; Mayr 2009, 2014c)
Trogonidae	<i>Paratrogon gallicus</i>	(E)	21.70	19.50	(Mlíkovský 2002; Mayr 2011)
Upupidae	<i>Upupa</i> sp.	(E)	19.50	17.2	(Mlíkovský 2002)
Phoeniculidae	<i>Phirriculus pinicola</i>	(E)	21.7	16.40	(Mlíkovský 2002; Mayr 2011)
Bucerotidae AO	<i>Tockus</i> sp.	(F)	15.00	14.00	(Brunet 1971; Boev

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	<i>Bucorvus brailloni</i>		11.62	5.30	and Kovachev 2007; Mayr 2014b)
Bucerotidae	<i>Euroceros bulgaricus</i>	(E)	8.90	7.40	(Boev and Kovachev 2007; Mayr 2011)
Meropidae	<i>Merops radoboyensis</i>	(E)	13.10	0.00	(Mlikovský 2002)
Coraciidae	<i>Microracias chenevali</i>	(E)	21.7	19.5	(Mourer-Chauviré et al. 2013a)
Todidae AO	<i>Palaeotodus</i> sp.	(N)(E)	38.00	28.10	(Mayr 2009; Mayr and Micklich 2010)
Alcediniformes AO	<i>Quasisyndactylus longibrachis</i>	(E)	47.80	38.00	(Mayr 2009, 2014c)
Momotidae AO	<i>Protornis glarniensis</i>	(E)	33.90	28.10	(Mlikovský 2002; Mayr 2009, 2011)
Momotidae	Momotidae indet.	(N)	10.3	4.90	(Becker 1986; Mayr 2011)
Alcedinidae	<i>Alcedo atthis</i>	(E)	0.126	0.00	(Mlikovský 2002; Sanchez Marco 2004)
Ramphastidae AO	<i>Rupelramphastoides knopfi</i>	(E)	28.10	23.03	(Mayr 2009, 2011)
Ramphastidae	<i>Capitonides</i> sp.	(E)	20.44	13.00	(Mayr and Gregorová 2012)
Indicatoridae	<i>Indicatoridae</i> indet.	(F)	5.333	3.66	(Olson 1985; Mayr and Gregorová 2012)
Picidae	<i>Piculoides saulcetensis</i>	(E)	23.03	20.5	(De Pietri et al. 2011b)
Coliidae AO	<i>Mesillacoliulus brevidactylus</i>	(E)	48.60	46.0	(Zelenkov and Dyke 2008; Ksepka and Clarke 2010b; Mayr 2013)
	<i>Celericolius acriala</i>	(N)	52.60	50.6	
Coliidae	<i>Limnatornis paludicola</i>	(E)	21.70	19.5	(Mourer-Chauviré 2008; Zelenkov and Dyke 2008; Mayr 2013)
	Coliidae indet.	(F)	23.03	20.4	
Cariamidae	<i>Noriegavis santacrucensis</i>	(S)	23.03	16.00	(Noriega et al. 2009; Mayr and Noriega 2013)
Falconidae AO	Falconidae indet.	(T)	47.80	41.30	(Tambussi et al. 1995; Noriega et al. 2011)
Falconidae	<i>Badiostes patagonicus</i>	(S)	15.97	11.62	(Becker 1987; Olson 1985; Suárez and Olson 2001; Martín Cenizo et al. 2012)
	<i>Thegornis musculosus</i>	(S)	16.5	16.0	
Cacatuidae	<i>Cacatua</i> sp.	(U)	15.97	11.62	(Boles 1993; Waterhouse 2006)
Psittacidae	<i>Nelepsittacus daphneleae</i>	(Z)	19	16	(Ksepka et al. 2011; Worthy et al. 2012)
Passeriformes	Passeriformes indet.	(U)	55.00	47.8	(Mayr 2009, 2014c)

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Hemiprocnidae	<i>Family without fossil record</i>	(A) (I)	0.01	0.00	(Del Hoyo et al. 1999; Ksepka et al. 2013)
Mesitornithidae	<i>Family without fossil record</i>	(M)	0.01	0.00	(Del Hoyo et al. 1996)
Psophiidae	<i>Family without fossil record</i>	(S)	0.01	0.00	(Del Hoyo et al. 1996; Ribas et al. 2011)
Chionidae	<i>Family without fossil record</i>	(S)(T)	0.01	0.00	(Del Hoyo et al. 1996)
Pluvianellidae	<i>Family without fossil record</i>	(S)	0.01	0.00	(Del Hoyo et al. 1996)
Pluvianidae	<i>Family without fossil record</i>	(F)	0.01	0.00	(Del Hoyo et al. 1996)
Ibidorhynchidae	<i>Family without fossil record</i>	(A)	0.01	0.00	(Del Hoyo et al. 1996)
Thinocoridae	<i>Family without fossil record</i>	(S)	0.01	0.00	(Del Hoyo et al. 1996)
Dromadidae	<i>Family without fossil record</i>	(F)(A)	0.01	0.00	(Del Hoyo et al. 1996)
Brachypteraciidae	<i>Family without fossil record</i>	(M)	0.01	0.00	(Del Hoyo et al. 2001)
Galbulidae	<i>Family without fossil record</i>	(N)(S)	0.01	0.00	(Del Hoyo et al. 2002)
Bucconidae	<i>Family without fossil record</i>	(N)(S)	0.01	0.00	(Del Hoyo et al. 2002)

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Appendix 3.8.3.

Table S3a. Areas definition for each node in Neornithes (1 - 0.5 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand. 1 y 2 (*italics*): Opisthocomiformes.

Node	Probability of combinations % (until 50%)	Defined areas
1	SFTU=38.12; SFT=18.48	S F T U
2	ST=15.35; SFT=9.49; NST=8.58; S=8.31; NSTZ=7.72; SFTU=7.66	S T
3	NSFEAU=63.07	N S F E A U
1	S=84.30	S
2	S=100.00	S
4	S=100.00	S
5	S=100.00	S
6	SFMI=51.51	S F M I
7	S=100.00	S
8	S=100.00	S
9	S=100.00	S
10	S=9.59; NS=4.93; SE=4.54; SF=3.82; SZ=3.12; SA=3.06; NSE=3.05; ST=2.74; NSF=2.64; SU=2.46; SFE=2.45; NSZ=2.38; NSA=2.24; SEZ=2.20; NSU=2.09; SEA=2.08	S

Table S3b. Areas definition for each node in Neornithes (1 - 0.25 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand. 1 y 2 (*italics*): Opisthocomiformes.

Node	Probability of combinations % (until 50%)	Defined areas
1	SFTU=46.34; SETU=20.78	S F T U
2	ST=17.83; S=12.52; SFTU=9.98; SFT=9.97	S T
3	NSFEAU=61.29	N S F E A U
1	S=100.00	S
2	S=100.00	S
4	S=100.00	S
5	S=100.00	S
6	SFMI=49.03; SFM=17.67	S F M I
7	S=100.00	S
8	S=100.00	S
9	S=100.00	S
10	S=17.64; SF=7.09; NS=6.94; SE=6.93; SZ=6.44; SA=4.76; SFZ=3.95	S

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Table S3c. Areas definition for each node in Neornithes (1 - 0.5 - 0 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand. 1 y 2 (*italics*): Opisthocomiformes.

Node	Probability of combinations % (until 50%)	Defined areas
1	FT=6.51; FTU=4.47; SFT=4.00; SFTU=3.37; T=2.95; FTUZ=2.69; FET=2.22; SFTUZ=2.12; FTZ=1.71; TU=1.69; ST=1.50; F=1.28; STU=1.18; SFTZ=1.08; TUZ=1.01; FTM=0.95; SFET=0.93; NSE=0.85; SE=0.84; FEAT=0.83; SET=0.81; SF=0.79; FETU=0.77; STUZ=0.76; FU=0.74; ET=0.74; NSEA=0.65; TZ=0.62; SFETU=0.61; SETU=0.60; SFU=0.56; NSFEA=0.56	T F
2	TUZ=1.77; STUZ=1.39; T=1.26; ST=1.22; NSFEATUZI=1.09; S=1.02; NSFEATI=1.01; TZ=1.00; TU=0.98; NSFEATUZ=0.96; NSFEAT=0.93; STZ=0.86; STU=0.84; UZ=0.75; NSFEATZI=0.68; NSFEATUI=0.66; NSFEATZ=0.61; NSFEAI=0.61; NSFEATU=0.60; FTUZ=0.59; NFEATUZI=0.59; NSEATUZI=0.57; NSFEA=0.56; NSFEATUZMI=0.55; U=0.53; NFEATUZ=0.52; NSEATUZ=0.52; NSEAI=0.50; SFTUZ=0.50; Z=0.50; NFEAI=0.49; NSFEATMI=0.49; NSEA=0.49; NSEATI=0.48; NFEATI=0.48; NSTUZ=0.47; NSFEATUZM=0.47; FT=0.46; NSEAT=0.46; SFT=0.46; NFEA=0.46; NFEAT=0.45; NSFEATM=0.44; NST=0.43; NS=0.43; NSFATUZI=0.37; FTZ=0.36; NFEATZI=0.35; FTU=0.35; NSEATZI=0.35; NEAI=0.34; NSFATI=0.34; NFEATUI=0.34; NSEATUI=0.34; NSFATUZ=0.34; NSFEATZMI=0.34; SFEATUZI=0.34; NSFETUZ=0.33; NSFEATUMI=0.33; NSFAT=0.33; NSFET=0.33; NEA=0.32; NSEATZ=0.32; SFTZ=0.32; NFEATZ=0.32; NSEATU=0.31; SFTU=0.31; SFEATUZ=0.31; NFEATU=0.31; SUZ=0.31; NSTZ=0.31; SFEATI=0.30; NEATUZI=0.30; NSFEATZM=0.30; NFEATUZMI=0.29; NSATUZI=0.29; SFEAT=0.29; NSFEATUM=0.29; NSTU=0.29; NSATUZ=0.29; FEATUZI=0.28; NEATUZ=0.27; FEATUZ=0.27; NSFEAMI=0.27; NSA=0.27; NSETUZ=0.26; NSAT=0.26; NSAI=0.26; NFEATUZM=0.25; NSFTUZ=0.25; NSATI=0.25; NSFT=0.24; NSE=0.24; NSFEAM=0.24; NSET=0.24; NFEATMI=0.23; NSFATZI=0.23; SFETUZ=0.23; FETUZ=0.22; NSFATUI=0.22; SZ=0.22; FEAT=0.22; FEATI=0.22; FTUZM=0.22; NSFATZ=0.22; SFET=0.22; SU=0.21; NSFETZ=0.21; NSFATU=0.21; SFEATZI=0.21;	N S F E A T

NSFEAUZI=0.21; NSFETU=0.21; NFEATM=0.21;
NFEAMI=0.20; SFEATUI=0.20; SFTUZM=0.20; TUZM=0.20;
SFEATZ=0.20; NFATUZI=0.20

3 NSFEATU=3.98; NSFEATUZ=3.08; NSFEATUI=2.32; N S F E A T U Z
NSFEATUZI=1.79; NSFEAT=1.48; NFEATUZ=1.46;
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NSEATU=1.18; NSFETU=1.17; NFEATZ=1.14;
NSFETUZ=0.98; SFEATU=0.97; NSEATUZ=0.97;
NSFEAUZ=0.94; NSFATU=0.94; NSFEATUM=0.89;
NSFEATI=0.84; NFEATUZI=0.82; NFEATUI=0.80;
NSFEAUI=0.78; NFEAZ=0.74; SFEATUZ=0.73;
NSFATUZ=0.73; NFEAT=0.73; NSFEATUZM=0.70;
NSFEATZI=0.70; NFEAU=0.68; NSEATUI=0.67;
NFEAUZ=0.66; NFEATZI=0.59; NSEATUZI=0.55;
SFEATUI=0.55; NSFEAUZI=0.54; NSFATUI=0.53;
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FEATUZ=0.45; NEATUZ=0.45; NSFTU=0.44; NSETU=0.42;
NFETU=0.42; SFEATUZI=0.42; FEATU=0.42;
NSFEATUZMI=0.42; NSFATUZI=0.41; NSEATZ=0.40;
NFEATI=0.39; NSEAU=0.39; NEATU=0.39; NSETUZ=0.38;
NFEAUI=0.38; NSFTUZ=0.38; NSEAT=0.38; SFETUZ=0.37;
FEATZ=0.37; NSFEU=0.37

1 NEA=2.94; NSFEA=2.27; S=2.04; NFEA=1.93; NEAI=1.71; N S F E A
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SFEA=0.66; NSE=0.66; NSFE=0.62; NSFEATMI=0.58;
NFEAT=0.58; NFA=0.57; FEAI=0.56; NSFAT=0.55; TU=0.55;
NSFEATM=0.55; NSEAT=0.54; NSFEATUZI=0.52; I=0.51;
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NSFEAM=1.57; NSFEATMI=1.53; EAI=1.53; NFEAMI=1.43;

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4	NEA=5.65; NFEA=4.55; NSFEA=4.31; NEAI=3.54; NSFEAT=3.01; NFEAI=2.81; EA=2.67; NA=2.62; NSEA=2.57; NSFEAI=2.53; FEA=2.43; NAI=1.87; EAI=1.84; NSFEATI=1.79; AI=1.75; NE=1.68; S=1.65; A=1.64; E=1.62; N=1.58	N E A
5	F=14.35; A=11.90; E=11.11; N=10.54	Indet.
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7	F=13.70; A=11.45; E=10.50; N=9.93; S=8.84	Indet.
8	NEA=5.83; F=5.25; E=4.51; EA=4.49; NA=4.32; N=4.27; S=4.19; A=3.95; NFEA=3.27; FEA=2.99; T=2.54; NE=2.45; M=2.43	Indet.
9	NEA=4.28; NFEA=3.30; NSFEA=3.00; NSFEATMI=2.64; NSFEATUZMI=2.60; EA=2.14; NA=2.06; NSFEAT=2.06; FEA=1.92; NSFEATM=1.88; NSEA=1.82; NSFEATZMI=1.77; NSFEAMI=1.58; NSFEATUMI=1.55; E=1.55; F=1.55; S=1.55; N=1.50; NSFEAM=1.46; NE=1.40; NSFEATI=1.39; NFEAMI=1.36; NSFEATUZM=1.34; NFEAI=1.29; NFEAM=1.28; FM=1.24; NSFEAI=1.23; A=1.21; SFT=1.20; M=1.19	N S F E A
10	NFEAT=0.12; NFEA=0.12; FEAT=0.12; NFAT=0.12; NEAT=0.12; NSFEAT=0.12; NSFEA=0.12; SFEAT=0.11; NSEAT=0.11; NSFAT=0.11; NFEATZ=0.11; NFET=0.11; NFEATI=0.11; SFEA=0.11; NFEAZ=0.11; NFA=0.11; NSFA=0.11; FEA=0.11; NFEAI=0.11; NSFEATI=0.11; NSFEATZ=0.11; NSEA=0.11; NSFET=0.11; EAT=0.11; SEAT=0.11; FEATZ=0.11; NEATZ=0.11; NFATZ=0.11; NSFEAZ=0.11; NEATI=0.11; NSFEAI=0.11; FAT=0.11; NFATI=0.11; FEATI=0.11; NFEATU=0.11; NAT=0.11; SFAT=0.11; NSAT=0.11; SFEATZ=0.11; NSEATZ=0.11; NSEATI=0.11; SFEATI=0.11; NEA=0.11; NFAZ=0.11; FEAZ=0.11; NSFATZ=0.11; NSFEATU=0.11; NSFATI=0.11;	N S F E A T

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 NSFETZI=0.11; NSEATUI=0.11; NSFSAZM=0.11;
 NSFSAZI=0.11; SFEATUI=0.11; NFEAMI=0.11; SEATU=0.11;
 NSETZ=0.11; NSFATUZ=0.11; NSETI=0.11; NSFATUZI=0.11;
 NEAU=0.11; NETI=0.11; NFEATUM=0.11; NSFATUI=0.11;
 NFETM=0.11; NSA=0.11; SEATZI=0.11; SEAI=0.11;
 EATZI=0.11; NSFETM=0.11; NSFATUM=0.11; SFAZ=0.11;
 SFEAM=0.11; NSAZ=0.11; EATU=0.11; SFETZ=0.11;
 NFEATZMI=0.11; NEATZM=0.11; NSATU=0.11; FETZ=0.11;
 NATZI=0.11; NSFAM=0.11; NSEAM=0.11; NFTZ=0.11;
 NEATMI=0.11; FEATZM=0.11; SFATU=0.11; SFETI=0.11;
 NSEATMI=0.11; NSATZI=0.11; NSAI=0.11; NSEATZM=0.11;
 NFATZM=0.11; NSFATZMI=0.11; SFEATZM=0.11;
 NFEAUZI=0.11; SFEATMI=0.11; NSFTZ=0.11; NFATMI=0.11;
 FEATMI=0.11; NATU=0.11; NFTI=0.11; NSFSAUZI=0.11;
 SFAI=0.11; NSFATZM=0.11; NSFTI=0.11; FATU=0.11;

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NSFATMI=0.11; NSFEU=0.11; SFEAUZ=0.11; NSFEZI=0.11;
NFEZI=0.11; SFATZI=0.11; NFAM=0.11; NFETUZ=0.11;
FATZI=0.11; SAT=0.11; NSEAUZ=0.11; SFEAUI=0.11;
FETI=0.11; NFETUI=0.11; NSFAUZ=0.11; SEATM=0.11;
NSEAUI=0.11; FEAUZ=0.11; NSFETUZ=0.11; NFAUZ=0.11;
NSFAUI=0.11; NSFETUI=0.11; FA=0.11; NEAUZ=0.10;
NFAUI=0.10; NEATUZI=0.10; NSFEAUM=0.10; FEAUI=0.10;
NSEATUZI=0.10; FEATUZI=0.10; NFEU=0.10; NEAM=0.10;
NSFEAZMI=0.10; SFEATUZI=0.10; NEAUI=0.10;
NSATM=0.10; NFEAUM=0.10; NFEAZMI=0.10;
NFATUZI=0.10; NFEATUZM=0.10; FEAM=0.10;
NSFEATUZM=0.10; NFEATUMI=0.10; NSFATUZI=0.10;
NSFEATUMI=0.10; SEATUZ=0.10; SEAZI=0.10; SFATM=0.10;
NATM=0.10; SEATUI=0.10; NSETZI=0.10; SFEAZM=0.10;
NFETZM=0.10; NSFETZM=0.10; EATM=0.10; NSEAZM=0.10;
NSFETMI=0.10; NSEATUM=0.10; SFEATUM=0.10;
NETZI=0.10; NSEAMI=0.10; NFETMI=0.10; SFEAMI=0.10;
FAZ=0.10; NSETU=0.10; NSF AZM=0.10; NSEATZMI=0.10;
NEATUM=0.10; NEATZMI=0.10; EATUZ=0.10; NSFEM=0.10;
SFEATZMI=0.10; NSEZ=0.10; NSATUZ=0.10; NSFAMI=0.10;
FEATUM=0.10; SATZ=0.10; NSFATUM=0.10; NSAZI=0.10;
NSATUI=0.10; NFATUM=0.10; EATUI=0.10; FEATZMI=0.10;
SATI=0.10; NSFATZMI=0.10; NFATZMI=0.10; SFATUZ=0.10;
SFETZI=0.10; NSFEUZ=0.10; NFAZM=0.10; SFAZI=0.10;
SFETU=0.10; NATUZ=0.10; NATUI=0.10; SFEZ=0.10;
SFATUI=0.10; NEAZM=0.10; FEAZM=0.10; SFE=0.10;
NSFEUI=0.10; SFEAUZI=0.10; NSEAUZI=0.10; SEAU=0.10;
NSFTZI=0.10; NSFETUZI=0.10; FATM=0.10; NFETUZI=0.10;
NSFEAUZM=0.10; NSEI=0.10; SEATZM=0.10; NSFAUZI=0.10;
FATUZ=0.10; NFEUZ=0.10; NSFEAUMI=0.10; NFAMI=0.10;
NSFTU=0.10; NFTZI=0.10; SEATMI=0.10; NSFEATUZMI=0.10;
FETZI=0.10; NFEAUZM=0.10; NFEATUZMI=0.10;
NEAMI=0.10; EAZ=0.10; NETU=0.10; FATUI=0.10;
NSFZ=0.10; NEAUZI=0.10; FEAUZI=0.10; NFAUZI=0.10;
SFAU=0.10; NFEUI=0.10; NFEAUMI=0.10; NAZI=0.10;
EA=0.10; FEAMI=0.10; EAZI=0.10; NSATZM=0.10; AT=0.10;
NSATMI=0.10; NSETM=0.10; EAI=0.10; NFEM=0.10;
SFEI=0.10; NSF=0.10; FAI=0.10; NSEATUZM=0.10; NSE=0.10;
NSFI=0.10; FETU=0.10; NAZ=0.10; SFEATUZM=0.10;
EATZM=0.10; SEATUZI=0.10; NSFETZMI=0.10; NFTU=0.10;
NSEATUMI=0.10; NSFETUM=0.10; SFATZM=0.10;
NSAU=0.10; NSEAZMI=0.10; SFEAZMI=0.10;

SFEATUMI=0.10; NSFEZM=0.10; NEATUZM=0.10;
NSFATUZM=0.10; NFETZMI=0.10; NATZM=0.10;
NSETUZ=0.10; SFATMI=0.10; NSETUI=0.10; EATMI=0.10;
NEATUMI=0.10; NSFEMI=0.10; FEATUZM=0.10;
NSFAZMI=0.10; NSFATUMI=0.10; SFEAUM=0.10;
NFETUM=0.10; NFATUZM=0.10; NATMI=0.10;
NSATUZI=0.10; FAZI=0.10; SEAUZ=0.10; FEATUMI=0.10;
NSEAUM=0.10; NA=0.10; SFETM=0.10; NFATUMI=0.10;
EATUZI=0.10; NSEZI=0.10; NSFAUM=0.10;
NSFEAUZMI=0.10; SEAUI=0.10; SATZI=0.10; NSFEUZI=0.10;
SFETUZ=0.10; SFATUZI=0.10; NEAZMI=0.10; NSFTM=0.10;
NATUZI=0.10; FATZM=0.10; NFAZMI=0.10; NETM=0.10;
SFETUI=0.10; NFEZM=0.10; NETUZ=0.10; FEAZMI=0.10;
NFEAUZMI=0.10; NETUI=0.10; NAI=0.10; SEATZMI=0.10;
NSFTUZ=0.10; SFAUZ=0.10; SFEZI=0.10; NSAUZ=0.10;
NSFTUI=0.10; NFEUZI=0.10; NSAUI=0.10; FATMI=0.10;
SET=0.10; NSEATUZMI=0.10; SEATUM=0.10; SETZ=0.10;
SFAUI=0.10; FATUZI=0.10; NSETZM=0.10; NSATZMI=0.10;
SFEATUZMI=0.10; NFEMI=0.10; SEAM=0.10; NSETMI=0.10;
NSFETUZM=0.10; NSFZI=0.10; ATZ=0.10; NFAUM=0.10;
NSFETUMI=0.10; NSFATUZMI=0.10; NEATUZMI=0.10;
FETUZ=0.10; FEAUM=0.10; NFTUZ=0.10; SETI=0.10;
SFEAUZM=0.10; NSAM=0.10; NSFEZMI=0.10; NFTM=0.10;
NSEAUZM=0.10; SFATZMI=0.10; NSETUZI=0.10;
NEAUM=0.10; NSATUM=0.10; EATZMI=0.10;
NFETUZM=0.10; NFTUI=0.10; FEATUZMI=0.10; FETUI=0.10;
ATI=0.10; NFATUZMI=0.10; NSEAUMI=0.10; SFEAUMI=0.10;
SATU=0.10; NSFAUZM=0.10; NEZI=0.10

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Table S3d. Areas definition for each node in Neornithes (1 - 0.1 - 0 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand. 1 y 2 (*italics*): Opisthocomiformes.

Node	Probability of combinations % (until 50%)	Defined areas
1	SFTU=40.09; SFT=21.12	S F T U
2	ST=20.11; SFT=12.96; SFTU=8.75; STZ=8.09; T=6.59	S T
3	SFTU=15.41; SFETU=12.58; SFEATU=12.26; NSFETU=7.39; SFEATUI=3.59	S F E T U
1	S=41.64; SF=38.32	S F
2	S=100.00	S
4	S=80.11	S
5	S=81.50	S
6	NSFEAMI=14.66; NSFAMI=14.37; SFAMI=10.04; NSFMI=8.53 SFEAMI=7.52	N S F A M I
7	S=71.55	S
8	S=54.09	S
9	ST=37.12; S=31.63	S T
10	T=1.58; ST=1.18; STU=0.99; STZ=0.94; TU=0.86; TZ=0.82; STUZ=0.82; SFT=0.74; SFTU=0.73; SFTZ=0.69; FT=0.68; TUZ=0.66; SFTUZ=0.63; STUM=0.62; FTU=0.62; FTZ=0.59; STZM=0.58; STUZM=0.57; STM=0.56; S=0.56; FTUZ=0.55; STUI=0.53; STZI=0.52; STI=0.50; SFTUM=0.50; STUZI=0.49; SU=0.48; SFTZM=0.47; SFTUZM=0.47; SZ=0.47; SFTM=0.45; TUM=0.45; TUZM=0.45; SUZ=0.44; NSTU=0.44; NSTZ=0.44; TM=0.44; TZM=0.43; SFTUI=0.43; SFTZI=0.43; SETU=0.43; SETZ=0.43; SFTUZI=0.42; NSTUZ=0.41; TI=0.41; TZI=0.41; SATU=0.40; TUI=0.40; SATZ=0.40; NST=0.40; SETUZ=0.40; FTUM=0.40; SFTI=0.40; SFU=0.40; TUZI=0.40; SFUZ=0.39; FTUZM=0.39; FTZM=0.39; SATUZ=0.39; SFZ=0.38; SET=0.38; NSFTU=0.38; STUMI=0.37; STUZMI=0.37; NSFTZ=0.37; SFETU=0.37; STZMI=0.37; SFETZ=0.37; NSFTUZ=0.36; SAT=0.36; FTUI=0.36; SFETUZ=0.36; FTZI=0.36; SFATU=0.35; SFATZ=0.35; FTUZI=0.35; FTM=0.35; SFATUZ=0.34; ETU=0.34; ATZ=0.34; SF=0.34; NSFT=0.34; NTU=0.33; NTUZ=0.33; SFET=0.33; ATU=0.33; SFTUZMI=0.33; NT=0.33; SFTUMI=0.33; SFTZMI=0.32; ETUZ=0.32; FTI=0.32; STMI=0.32; ETZ=0.32; SFAT=0.32; NSTZI=0.31; NTZ=0.31; NSATZ=0.31; NSATUZ=0.31; NSTUZI=0.31; ATUZ=0.31; NSATU=0.31; NFTZ=0.31; NSETZ=0.31; NSTUI=0.31; SEATZ=0.31; NSETUZ=0.31; NFTU=0.31; SETZI=0.31; SEATUZ=0.31; NSETU=0.30	S T U Z

Appendix 3.8.4.

Table S4a. Areas definition for each node in Paleognathae (1 - 0.5 - 0.1 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	F=50.45	F
2	F=42.76; FE=30.68	F E
3	Z=100	Z
4	SZ=100	S Z
5	NSZ=36.94; SEZ=36.03	S Z N E
6	U=100.00	U
7	UZ=100.00	U Z
8	NSZ=24.46; SEZ=24.37; NSUZ=13.42	S Z N
9	NSZ=27.01; SEZ=26.02	S Z N E
10	NSFZ=19.35; SFEZ=18.16; NSFUZ=10.53; SFEUZ=9.71	S Z F N E

Table S4b. Areas definition for each node in Paleognathae (1 - 0.25 - 0.1 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	F=50.52	F
2	F=47.16; FE=25.56	F E
3	Z=100	Z
4	SZ=100	S Z
5	NSZ=23.90; SEZ=23.29; Z=10.00	S Z
6	U=100	U
7	UZ=100	U Z
8	NSZ=17.17; SEZ=16.97; NSUZ=9.44; SEUZ=9.18	S Z N E
9	NSZ=22.25; SEZ=21.56; NSUZ=12.53	S Z N
10	NSFZ=16.08; SFEZ=15.36; NSFUZ=9.24; SFEUZ=8.61; SFZ=7.48	S F Z N

Table S4c. Areas definition for each node in Paleognathae (1 - 0.5 - 0 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	F=43.02; FE=35.38	F E
2	F=37.21; FE=33.25	F E
3	Z=100.00	Z
4	SZ=100.00	S Z
5	NSZ=51.53	N S Z
6	U=100.00	U
7	UZ=100.00	U Z
8	NSZ=31.42; SEZ=30.43	S Z N E
9	NSZ=32.20; SEZ=29.92	S Z N E
10	NSFZ=22.60; SFEZ=20.23; NSFUZ=11.56	S F Z N

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Table S4d. Areas definition for each node in Paleognathae (1 - 0.1 - 0 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	F=74.25	F
2	F=58.37	F
3	Z=100	Z
4	SZ=100	S Z
5	NSZ=43.12; SEZ=36.74	S Z N E
6	U=100	U
7	UZ=100	U Z
8	NSZ=26.01; SEZ=22.52; NSUZ=14.82	S Z N
9	NSZ=26.47; SEZ=22.24; NSUZ=14.90	S Z N
10	NSFZ=23.98; SFEZ=19.85; NSFUZ=13.67	S F Z N

Appendix 3.8.5.

Table S5a. Areas definition for each node in Galloanseres (1 - 0.5 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	E=25.00; N=23.67; A=10.44	E
2	S=100.00	S
3	U=28.60; S=26.86	U S
4	SU=100.00	S U
5	S=86.56	S
6	S=100.00	S
7	S=40.90; SU=26.63	S U
8	S=40.35; SU=27.43	S U
9	SU=41.30; SEU=15.64	S U
10	N=100.00	N
11	F=43.75; A=39.39	F A
12	NFEAIM=15.54; NFEAI=15.02; E=13.03; NFEA=12.27	E N F A I
13	NFE=11.59; NFEA=11.38; NE=9.54; NEA=9.49; N=9.06	N E
14	NFEA=17.54; NEA=15.28; NFE=11.83; NFEAI=7.68	N E A F
15	NFEA=21.62; NEA=19.08; NFE=15.14	N E A F
16	NFEA=35.89; NEA=27.51	N E A F
17	E=100.00	E
18	E=100.00	E
19	E=100.00	E
20	E=100.00	E
21	SEU=61.84	S E U
22	NSEU=29.29; SEU=21.66; SEAU=14.42	S E U N

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Table S5b. Areas definition for each node in Galloanseres (1 - 0.25 – 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	E=24.18; N=23.31; NA=13.09	N
2	S=100.00	S
3	U=38.70; S=22.87	U
4	SU=100.00	S U
5	S=83.17	S
6	S=87.79	S
7	S=36.31; SU=28.62	S U
8	S=33.32; SU=28.28	S U
9	SU=39.60; STU=15.83	S U
10	N=100.00	N
11	F=38.07; A=34.42	F A
12	NFEAIM=17.27; NFEAI=16.30; NEA=12.53; NFEA=11.94	N E A F I
13	N=12.52; NFEA=10.97; NE=10.37; NEA=9.65; NFE=9.26	N E
14	NEA=15.53; NFEA=14.91; NFE=9.03; NFEAI=8.17; NFEAIM=7.28	N E A F
15	NEA=18.67; NFEA=18.46; NFE=11.81; NFEAI=8.47	N E A F
16	NFEA=27.70; NEA=27.15; NFEAI=10.29	N E A F
17	E=100.00	E
18	E=100.00	E
19	E=100.00	E
20	E=100.00	E
21	SEU=53.08	S E U
22	NSEU=25.56; SEU=18.90; SEAU=15.29	S E U N

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Table S5c. Areas definition for each node in Galloanseres (1 - 0.5 - 0 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	N=27.92; E=17.77; NE=11.52	N E
2	S=100.00	S
3	U=100.00	U
4	SU=100.00	S U
5	SU=87.42	S U
6	SU=57.43	S U
7	SU=63.47	S U
8	SU=62.30	S U
9	SU=64.05	S U
10	N=100.00	N
11	F=35.26; A=35.09	F A
12	E=27.64; EA=13.74; NEA=10.72	E
13	E=27.34; A=17.02; NFE=12.35	E
14	A=13.34; E=11.59; NFE=10.65; NFEA=9.93; EA=8.42	A E
15	NA=17.95; NEA=16.82; NFEA=16.45	N E A
16	NFEA=27.14; NEA=26.16	N E A F
17	E=67.26	E
18	E=69.15	E
19	E=68.83	E
20	E=68.76	E
21	SEU=34.54; NSU=18.67	S U E
22	NSEU=19.05; SEU=13.57; NSETU=12.49; NSU=9.92	S E U N

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Table S5d. Areas definition for each node in Galloanseres (1 - 0.1 - 0 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	N=18.08; NEA=13.34; NA=12.58; E=11.79	N E A
2	S=100.00	S
3	U=100.00	U
4	SU=100.00	S U
5	SU=100.00	S U
6	SU=55.11	S U
7	SU=55.16	S U
8	SU=55.13	S U
9	SU=56.10	S U
10	N=100.00	N
11	E=34.87; A=26.30	E A
12	E=30.25; EA=18.38; NEA=17.35	E A
13	E=32.24; A=23.37	E
14	E=19.73; A=16.74; EA=10.98; NEA=8.64	E A
15	NE=19.75; NEA=18.81; NA=17.42	N E A
16	NEA=33.00; NFEA=14.35; NA=12.57	N E A
17	E=54.03	E
18	E=56.56	E
19	E=56.71	E
20	E=52.71	E
21	SEU=26.54; SETU=18.41; NSU=13.54	S U E
22	NSEU=11.81; NSETU=11.08; SEAU=8.68; SEU=8.54; SEATU=7.61; NSAU=6.80	S E U N

Appendix 3.8.6.

Table S6a. Areas definition for each node in Columbea (1 - 0.5 - 0.1 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	E=21.67; EM=12.46; FEM=9.81; FE=8.30	E M
2	EM=24.75; FEM=19.32; M=11.85	E M
3	SU=100.00	S U
4	SUM=36.34; SEU=22.61	S U
5	U=15.86; SU=10.42; IU=9.51; AU=9.21; FU=8.45	U
6	U=46.23; E=25.66	U E
7	U=45.51; E=32.01	U E
8	U=60.80	U
9	U=46.76; E=30.21	U E
10	SEU=18.85; SUM=16.52; SFU=10.63; SEUM=10.49	S U E M

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Table S6b. Areas definition for each node in Columbea (1 - 0.25-0.1 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	E=29.52; EM=18.83; M=10.18	E M
2	EM=34.46; M=14.44; FEM=11.92	E M
3	SU=100	S U
4	SUM=36.74; SEU=23.64	S U
5	U=19.84; SU=14.45; FU=11.72; IU=10.91	U
6	U=55.81	U
7	U=51.16	U
8	U=74.34	U
9	U=52.33	U
10	SEU=23.00; SUM=20.09; SEUM=11.86	S U E M

Table S6c. Areas definition for each node in Columbea (1 - 0.5-0 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	F=32.46; FM=13.46; FE=11.96	F
2	FM=43.53; FEM=24.16	F M
3	SU=100	S U
4	SUM=42.41; SFU=37.86	S U M F
5	AU=7.05; NEAIU=6.90; NFEAIU=6.75; NAIU=6.21; NAU=5.85; NEAU=5.26; NSFIAIU=4.98; NSFIAIU=4.71; U=4.44	U A N I E
6	U=37.95 A=21.62	U
7	U=43.34; A=27.46	U A
8	U=69.99	S U
9	U=44.29; A=26.82	U A
10	SFU=15.83; SUM=15.52; SAUM=11.01; SFAU=10.05	S U F M

Table S6d. Areas definition for each node in Columbea (1 - 0.1 - 0 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	F=57.63	F
2	FM=67.79	F M
3	SU=100	S U
4	SUZ=52.79	S U Z
5	NEAIU=32.90; NEAU=13.42; NFEAIU=12.74	N E A I U
6	U=100.00	U
7	U=71.21	U
8	U=87.86	U
9	U=70.51	U
10	SUM=26.77; SFU = 24.58	S U M

Appendix 3.8.7.

Table S7a. Areas definition for each node in Caprimulgimorphae (1 - 0.5 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=30.13; SE=21.65	S
2	SE=62.39	S E
3	E=100.00	E
4	E=49.16; EA=44.03	E A
5	E=100.00	E
6	EU=68.64	E U
7	E=29.83; EU=24.02	E
8	E=31.15; EU=26.55	E U
9	E=100.00	E
10	E=88.01	E
11	E=100.00	E
12	E=100.00	E
13	E=100.00	E
14	E=100.00	E
15	E=78.68	E
16	SE=47.23; E=29.65	E S
17	SE=50.04	S E

Table S7b. Areas definition for each node in Caprimulgimorphae (1 - 0.25 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	SE=25.66; S=24.70	S E
2	SE=58.77	S E
3	E=86.82	E
4	E=50.72	E
5	E=100.00	E
6	EU=69.38	E U
7	E=34.45; EU=23.47	E
8	E=36.24; EU=27.99	E U
9	E=100.00	E
10	E=87.21	E
11	E=100.00	E
12	E=100.00	E
13	E=100.00	E
14	E=100.00	E
15	E=82.32	E
16	SE=44.67; E=38.82	E S
17	SE=46.22; E=29.12	E S

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Table S7c. Areas definition for each node in Caprimulgimorphae (1 - 0.5 - 0 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	S=61.10	S
2	SE=30.46; NE=18.53; E=14.38	E S
3	E=72.05	E
4	E=58.22	E
5	E=100.00	E
6	EAU=31.93; EA=24.91	E A U
7	A=41.83; E=38.80	A E
8	E=41.22; EA=30.99	E A
9	E=100.00	E
10	E=77.22	E
11	E=100.00	E
12	E=100.00	E
13	E=100.00	E
14	E=100.00	E
15	E=45.94; SE=36.98	E S
16	SE=50.35	S E
17	SE=40.70; NSE=19.34	S E

Table S7d. Areas definition for each node in Caprimulgimorphae (1 - 0.1 - 0 Model).

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australia; (T) Antarctica; (M) Madagascar; (Z) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	S=61.61	S
2	SE=21.03; NEA=11.09; E=9.25; NA=8.35	E
3	E=24.42; A=23.54; EA=19.77	E A
4	EA=25.06; E=23.39; EAU=11.93	E A
5	E=40.76; A=39.29	E A
6	EAU=34.11; EU=22.29	E U A
7	A=67.51	A
8	A=60.49	A
9	A=50.90	A
10	A=54.83	A
11	A=52.10	A
12	A=57.03	A
13	A=55.61	A
14	A= 55.01	A
15	A=35.53; E=25.13	A E
16	SE=17.99; SEA=10.39; N=9.80; A=9.55; SA=7.70	S E A
17	SEA=11.65; SE=11.03; NSEA=8.99; NSE=6.86; SFEA=4.53; SEAI=4.04; NSFEA=3.99	S E A

Appendix 3.8.8.

Table S8a. Areas definition for each node in Otidimorphae (1 - 0.5 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	SFIM=100.00	S F I M
2	F=100.00	F
3	FEAIU=20.90; F=19.84; FEAI=11.44	F E A I
4	F=87.51	F
5	SFIM=100.00	S F I M

Table S8b. Areas definition for each node in Otidimorphae (1 - 0.25 - 0.1 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	SFIM=100.00	S F I M
2	F=100.00	F
3	F=24.94; FEAIU=17.21; FE=10.46	F E
4	F=100.00	F
5	SFIM=100.00	S F I M

Table S8c. Areas definition for each node in Otidimorphae (1 - 0.5 - 0 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	SFIM=100.00	S F I M
2	F=100.00	F
3	FEAIU=25.99; F=16.60, FEAI=12.41	F E A I U
4	F=85.37	F
5	SFIM=100.00	S F I M

Table S8d. Areas definition for each node in Otidimorpha (1 - 0.5 - 0 Model).

(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	SFIM=100.00	S F I M
2	F=100.00	F
3	F=31.02; FE=22.12	F
4	F=100.00	F
5	SFIM=100.00	S F I M

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Appendix 3.8.9.

Table S9a. Areas definition for each node in Cursoriomorphae - Gruiformes (1 - 0.5 - 0.1 Model).
(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	NS=66.42	N S
2	FE=100.00	F E
3	NE=42.19; E=27.15	N E
4	N=49.51; E=29.11	N E
5	N=42.97; SE=18.21	N
6	N=29.64; S=25.67	N S
7	FE=100.00	F E
8	NSFI=50.50	N S F I
9	FE=55.57	F E
10	FEZ=43.05; NFEZ=14.54	F E Z
11	FEZ=25.74; NFEZ=24.72	F E Z
12	NFEZ=27.86; NSF EZ=21.22; SFEZ=18.18	N E S F Z

Table S9b. Areas definition for each node in Cursoriomorphae - Gruiformes (1 - 0.25 - 0.1 Model).
(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	NS=62.51	N S
2	FE=100.00	F E
3	NE=29.66; E=25.84	N E
4	N=33.39; E=25.51	N E
5	N=32.07; SE=22.23	N
6	S=27.16; N=21.17; NS=19.06	N S
7	FE=100.00	F E
8	NSFI=44.38; NSF=22.91	N S F I
9	FE=59.38	F E
10	FEZ=50.19	F E Z
11	FEZ=27.28; NFEZ=25.41	N F E Z
12	NFEZ=26.23; NSF EZ=22.25; SFEZ=20.77	N F E Z S

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Table S9c. Areas definition for each node in Cursoriomorphae - Gruiformes (1 - 0.5 - 0 Model).
(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	NS=70.89	N S
2	FE=100.00	F E
3	NE=69.03	N E
4	N=58.75	N
5	N=53.94	N
6	N=37.86; NS=36.45	N S
7	FE=100.00	F E
8	NSFI=46.84; NSF AI=30.94	N S F A I
9	FE=50.22	F E
10	FEZ=45.43; NFEZ=18.30	F E Z
11	NFEZ=22.47; FEZ=21.11; FEAZ=7.73	F E Z
12	NFEZ=26.23; NSF EZ=13.30; NSF EIZ=10.50	N F E Z

Table S9d. Areas definition for each node in Cursoriomorphae - Gruiformes (1 - 0.1 - 0 Model).
(**N**) North and Central America; (**S**) South America; (**E**) Europe; (**A**) Asia; (**I**) India; (**F**) Africa; (**U**) Australia; (**T**) Antarctica; (**M**) Madagascar; (**Z**) Zealand

Node	Probability of combinations % (until 50%)	Defined areas
1	NS=82.95	N S
2	NA=41.81; N=23.61	N A
3	N=85.75	N
4	N=100.00	N
5	NS=54.33	N S
6	NS=49.82; N=29.14	N S
7	N=65.06	N
8	NSFA=51.35	N S A F
9	N=16.05; NSFA=8.71; NSF=7.67; NZ=6.12; NAZ=4.51; NFAZ=3.92; NSA=3.71	N
10	NZ=18.31; NSFAZ=8.95; NSFZ=8.40; NAZ=6.41; NFAZ=5.77; NFZ=5.47	N F Z
11	NZ=11.61; NSFAZ=6.41; NAZ=5.42; NEZ=4.97; NSFEAZ=4.68; NSFZ=4.42; NSF EZ=4.09; NFAZ=4.05; NFEAZ=4.00; NEAZ=3.93	N F A Z
12	NSFAZ=6.89; NZ=6.67; NSF EAZ=5.45; NSZ=5.18; NSFZ=4.92; NSFEZ=4.81; NSA Z=4.66; NSEZ=3.86; NSEAZ=3.64; NAZ=3.05; NEZ=2.63	N S Z

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Appendix 3.8.10.

Table S10a. Areas definition for each node in Cursoriomorphae - Charadriiformes (1 - 0.5 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	U =39.98; SU =29.92	S U
2	ST =85.75	S T
3	SU =37.68; SFU =22.51	S U
4	A =43.16; E =29.14	A E
5	NS =4.10; NAU =3.94; NSF =3.89; NF =3.52; NSFU =3.46; NA =3.13; NFAU =3.07; NSU =3.04; NSFUZ =2.96; N =2.91; NU =2.89; NSFAU =2.84; NSAU =2.80; NFU =2.73; NSFZ =2.56; NFA =2.40; NFUZ =2.36	N S F U
6	A =55.12	A
7	A =63.17	A
8	A =61.46	A
9	FA =32.44; A =26.19	F A
10	A =64.49	A
11	A =64.70	A
12	N =100.00	N
13	SU =56.68	S U
14	SFEAU =16.51; FEA =13.64; FEAU =12.21; SFEA =12.12	S F E A U
15	F =100.00	F
16	F =69.92	F
17	F =16.17; SF =8.81; SFU =8.06; S =6.29; FU =6.16; U =5.80	F
18	NSFU =5.94; NSF =5.29; NSFEAU =5.25; NSFAU =4.88; NFEAU =4.46; NSFE =4.43 NFAU =4.15 NSFEA =4.00 NSFA =3.73 NF =3.32 NSFEU =2.99 NFU =2.90	N S F A U
19	E =74.74	E
20	E =71.20	E
21	E =100.00	E
22	E =62.45	E
23	E =72.45	E
24	E =100.00	E
25	E =100.00	E
26	E =100.00	E
27	E =100.00	E
28	NSFEAU =6.06; NSFE =5.67; E =5.56; NSFEU =5.55; NFE =5.07; NSFEA =4.88; NFEAU =4.85; NFEA =4.56; FE =4.48; NEA =3.93	N F E A
29	NSFEAU =4.16 SFEAU =3.58 NSFEA =3.22 NFEAU =3.14 SFEA =2.62 NSFEU =2.51 SEAU =2.49 FEAU =2.22 NSFAU =2.15 SFEU =2.09 NSEAU =2.06 SFAU =1.99 NFEU =1.81 NFEA =1.76 NSFE =1.62 NSFA =1.57 NEAU =1.54 NFAU =1.53 NSEA =1.49 SEA =1.47 NSFEAUZ =1.35 NSFEAUZ =1.31 NSFEATU =1.29 SFEATU =1.25	N S F E A U

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Table S10b. Areas definition for each node in Cursoriomorphae - Charadriiformes (1 - 0.25 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	U=43.86; SU=27.17	S U
2	ST=85.12	S T
3	SU=39.58; SFU=23.89	S F U
4	E=39.21; A=32.10	E A
5	NF=5.56; NFU=4.64; NAU=4.41; NSF=4.40; NS=4.02; NSFU=3.98 NSFUZ=3.60; NFUZ=3.51; NFZ=3.41; NSU=3.39; NSFZ=3.06; N=2.60 NFAU=2.57; NSUZ=2.56	N S F U
6	A=38.42; E=30.71	A E
7	A=46.09; E=32.06	A E
8	A=43.43; F=21.65	A
9	FA=24.57; F=22.35; A=14.84	F A
10	A=46.32; E=27.43	A E
11	A=40.49; F=31.16	A F
12	N=100.00	N
13	SU=55.27	S U
14	SFEAU=17.91; FEAU=13.09; FEA=11.04; SFEA=10.92	S F E A U
15	F=100.00	F
16	F=55.97	F
17	F=18.09; U=13.81; S=9.22; SF=6.97; FU=6.82	F
18	NSFEAU=5.50; NSFAU=5.05; NFEAU=5.04; NFAU=4.86; NSFU=4.55; NSF=3.65; NAU=3.61; NFU=3.16; NSFEA=3.09; NSFE=2.99; NSFA=2.88; NSFEU=2.69; NEAU=2.68; NF=2.63	N S F E A U
19	E=78.40	E
20	E=83.56	E
21	E=100.00	E
22	E=56.21	E
23	E=68.79	E
24	E=87.90	E
25	E=100.00	E
26	E=100.00	E
27	E=100.00	E
28	E=6.39; NSFEAU=6.37; NFEAU=5.43; NSFEU=4.72; NSFEA=4.31; NFEA=4.26; EA=4.18; NSFE=4.16; NEA=4.05; FE=4.04	E N F A
29	NSFEAU=3.83; SFEAU=3.32; NSFEU=3.26; NFEAU=2.93; NSFEA=2.91; SFEA=2.51; SFEU=2.50; NFEU=2.42; FEAU=2.33; NSFE=2.13; SEAU=1.93 NSFAU=1.71; SFAU=1.65; NSEAU=1.64; NFEA=1.53; FEU=1.48; SFE=1.48; NFAU=1.27; NSFEAU=1.27; NSFEAUZ=1.22; NSFA=1.22; NSFEAU=1.21; SEA=1.18; NSFEATU=1.17; NEAU=1.14; NSEU=1.13	N S F E A U

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Table S10c. Areas definition for each node in Cursoriomorphae - Charadriiformes (1 - 0.5 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	SFU=24.30; SFAU=9.48; NSFAU=7.47; SFUZ=6.61; NSFEAU=6.31	S F U
2	ST=85.85	S T
3	SFTU=11.82; SFU=11.29; NSFAU=6.52; NSAU=5.67; NSFEAU=5.50; NSFU=4.88; SFAU=4.53	S U F
4	E=46.84; A=44.11	E A
5	NSFEAU=7.10; NSFAU=6.94; NSEAU=5.68; NSAU=5.32; NFEAU=4.57; NEAU=3.91; NSFU=3.77; NSEA=3.60; NSA=3.59; NSFEA=3.56; NFAU=3.47	N S F E A U
6	A=48.61; E=42.95	A E
7	A=50.35	A
8	A=48.83	A
9	E=19.48	E
10	A=51.05	A
11	A=63.09	A
12	N=76.98	N
13	SU=14.52; NA=14.28; NAU=14.05; NU=9.71	U A N
14	NFEA=13.14; NEA=10.05; NSFEA=8.79; NFEAU=7.65; FEA=6.76; NSEA=6.73	N F E A
15	A=34.66; F=29.80	A F
16	A=45.65; F=17.39	A
17	A=32.32; N=17.14; NA=11.44	A N
18	NA=14.38; N=12.27; NEA=10.26; NE=8.57; A=7.94	N A
19	E=75.91	E
20	E=82.17	E
21	E=86.13	E
22	E=81.46	E
23	E=100.00	E
24	E=100.00	E
25	E=100.00	E
26	E=100.00	E
27	E=100.00	E
28	NEA=20.32; E=18.00; NE=17.11	N E
29	SFEAU=2.40; NSFEAU=1.92; SEAU=1.82; SFEATU=1.72; NSEAU=1.67; NSFEU=1.40; SFEU=1.37; NSFEATU=1.34; NSFAU=1.14; SFEAUZ=1.12; SFEAUM=1.07; FEATU=1.05; SEATU=1.05; NSEATU=1.01; NSFETU=0.98; SEA=0.98; SEAUM=0.98; NSFEA=0.97; NSEA=0.97; NFEATU=0.96; SFETU=0.96; SFEA=0.94; NSFEAUZ=0.94; NSFEAUM=0.90; NSEU=0.90; SFEAIU=0.88; SFAU=0.88; SEU=0.88; SFEATUZ=0.88; NEAU=0.86; SFEATUM=0.84; NSEAUM=0.83; NFEAU=0.83; NSFEAIU=0.80; NEATU=0.79; NSFATU=0.79; NEA=0.77; SEAUZ=0.75; NSEAUZ=0.74; SFEAZ=0.74; NSFEATUZ=0.74; EATU=0.73; NSFEATUM=0.70; NFETU=0.69; SFEAITU=0.69; NSEAIU=0.67; NSFEAZ=0.67; SEATUM=0.67; SEAIU=0.66; NSFEUZ=0.66	A E U S F N

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Table S10c. Areas definition for each node in Cursoriomorphae - Charadriiformes (1 - 0.1 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	SFU=59.64	S F U
2	ST=82.29	S T
3	SFU=38.87; SFTU=21.40	S F U
4	E=48.58; A=36.46	E A
5	NEAU=10.03; NSEAU=8.53; NEAIU=5.46; NFEAU=5.01; NSFEAU=4.76; NSEAIU=4.65; NSFU=3.80; NSEU=3.75; NEU=3.59; NEAUZ=3.52	N S E A U
6	E=45.99; A=38.68	E A
7	E=47.66; A=39.10	E A
8	E=46.07; A=31.16	E A
9	E=30.89; EA=17.42; FE=10.45	E
10	E=54.93	E
11	A=47.97; E=33.94	A E
12	N=67.60	N
13	NU=27.16; SU=24.07	U N
14	EA=11.34; FEA=10.98; NFEA=8.92; NEA=7.89; E=7.17; NFEAU=6.25	F E A
15	A=31.47; F=28.53	A F
16	A=44.53; E=23.79	A
17	A=27.54; NAU=15.31; NEAU=7.95	A
18	NAU=11.85; NEAU=11.65; NA=10.96; NEA=8.36; A=6.81; NSAU=6.65	N A U
19	E=76.24	E
20	E=80.49	E
21	E=69.12	E
22	E=68.88	E
23	E=86.27	E
24	E=100.00	E
25	E=100.00	E
26	E=100.00	E
27	E=100.00	E
28	NEA=18.55; EA=15.54; E=11.21; NEAU=11.09	N E A
29	SFEAU=4.47; SFEATU=3.14; NSFEAU=2.96; SFEU=2.70; NSFEU=2.51; NSFEATU=2.07; SFEAUM=2.00; SFEAUZ=1.99; SEAU=1.91; SFEAIU=1.87; SFETU=1.85; NSFAU=1.77; NSFETU=1.75; SFAU=1.63; NSEAU=1.60; SFEATUZ=1.53; SFEATUM=1.52; NSFEAIU=1.50; NSFEA=1.44; NSFEAUM=1.43; SFEA=1.40; NSFEAUZ=1.40; SFEAITU=1.38; NSFATU=1.22; SFEIU=1.19; SFEUZ=1.15; SFEUM=1.15	S F E A U

3. Paleobiogeographic history

Appendix 3.8.11.

Table S11a. Areas definition for each node in Phaethontimorphae-Aequornithia (1 - 0.5 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=70.43	S
2	S=66.98	S
3	F=27.02; A=19.23; S=19.20	F
4	S=25.50; SU=11.32; NS=10.07; NSU=9.77	S
5	N=51.27	N
6	STZ=100.00	S T Z
7	NSTZ=100.00	N S T Z
8	S=81.05	S
9	S=81.88	S
10	S=86.82	S
11	S=43.51; SE=21.74	S
12	NS=30.41; NSE=18.54; NSA=17.39	N S
13	N=83.75	N
14	NSTZ=33.71; N=22.42	N S T Z
15	A=20.39; NA=12.78; FA=7.63; NEA=6.77; EA=5.84	A
16	N=36.90; NA=25.49	N A
17	NEA=15.80; EA=13.23; NE=10.25; NFEA=8.08; E=7.35	N E A
18	SFIU=25.73; SFAIU=16.94; SIU=9.45	S F I U
19	A=62.05	A
20	A=66.82	A
21	A=57.78	A
22	A=53.97	A
23	N=45.24; A=40.45	N A
24	A=52.95	A
25	N=100.00	N
26	NFEA=14.05; NEA=9.28; NFE=8.02; FEA=6.53; EA=5.54; NFEAI=5.47; NFEAU=5.19	N F E A
27	F=100.00	F
28	NFEA=21.12; NFE=12.20; FEA=11.03; FE=8.21	N F E A
29	N=54.42	N
30	NA=34.06; N=27.17	N A
31	N=63.30	N
32	N=55.33	N
33	N=63.18	N
34	N=79.80	N
35	N=72.26	N
36	NSATZ=24.95; NSTZ=12.20; NSAZ=7.83; NSU=7.16	N S A T Z

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Table S11b. Areas definition for each node in Phaethontimorphae-Aequornithia (1 - 0.25 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=81.53	S
2	S=67.05	S
3	F=32.00; S=25.07	F S
4	S=33.32; SU=14.65; SF=12.46	S
5	N=46.94; S=31.34	N S
6	STZ=100.00	S T Z
7	NSTZ=100.00	N S T Z
8	S=75.31	S
9	S=76.04	S
10	S=80.42	S
11	S=47.27; SE=16.53	S
12	NS=24.54; NSA=16.53; S=14.67	N S
13	N=82.86	N
14	NSTZ=39.79; N=20.18	N S T Z
15	A=15.76; NA=12.63; EA=6.24; NEA=6.17; F=5.78	A
16	N=41.71; NA=28.04	N A
17	NEA=20.59; EA=15.76; E=9.19; NE=9.03	N E A
18	SFIU=27.93; SFAIU=13.01; SIU=11.53	S F I U
19	A=53.75	A
20	A=58.09	A
21	A=54.37	A
22	A=49.68; N=42.08	A N
23	N=49.14; A=37.97	N A
24	A=45.13; NA=15.19	A
25	N=100.00	N
26	NFEA=13.21; NEA=7.08; NFEAU=6.96; NFEAI=6.24; NFE=6.15; FEA=5.92; F=5.88	N F E A
27	F=100.00	F
28	NFEA=19.30; FEA=9.59; NFEAU=9.24; NFE=9.01; NFEAI=8.52	N F E A
29	N=55.26	N
30	NA=36.63; N=27.68	N A
31	N=64.35	N
32	N=57.90	N
33	N=64.61	N
34	N=65.10	N
35	N=64.97	N
36	NSATZ=19.20; NSTZ=14.76; NSU=5.93; NSFU=5.05; NSZ=4.99; NS=4.87	N S T Z

3. Paleobiogeographic history

Table S11c. Areas definition for each node in Phaethontimorphae-Aequornithia (1 - 0.5 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	N=70.59	N
2	N=80.61	N
3	N=35.72; A=19.27	N
4	N=23.23; NA=14.07; NEA=10.79; NS=8.88	N
5	S=57.21	S
6	STZ=100.00	S T Z
7	STZ=41.42; NSTZ=41.42	N S T Z
8	S=53.61	S
9	N=45.05; S=35.58	N S
10	N=61.44	N
11	N=59.42	N
12	N=24.65; NS=15.35; NSA=10.52	N S
13	N=65.68	N
14	NSTZ=58.92	N S T Z
15	NEA=8.64; NFEA=7.76; NFEAI 5.57; NEAI 5.41; NA=5.23; N=4.64; NE=3.81; NSEA=3.43; FEA=3.42; E=3.34	N E A
16	N=35.04; NA=14.39; NEA=13.03	N A
17	NEA=12.69; E=9.26; NFEA=8.87; NE=7.22; EA=6.02; NEAU=6.01; NFEAU=5.46	N E A
18	NSFEAIU=15.11; NSFAIU=14.18; SFAIU=7.89; NSAU=6.10; SFEAIU=5.55; SAU=5.14	N S F A I U
19	N=53.52	N
20	N=55.09	N
21	N=56.39	N
22	N=58.52	N
23	N=61.38	N
24	N=18.07; E=15.24; NEA=11.65; NA=10.89	N E
25	N=61.75	N
26	E=22.17; NEA=10.51; NFEA=9.58; EA=8.15	E A
27	F=100.00	F
28	FE=20.33; NFEA=17.57; FEA=12.35	F E A
29	N=46.51; E=24.18	N
30	N=36.51; E=15.56	N
31	N=62.57	N
32	N=62.87	N
33	N=62.15	N
34	NSTZ=37.29; NSZ=23.09	N S T Z
35	NSTZ=40.87; NSZ=19.74	N S T Z
36	NSTZ=19.31; NSETZ=13.53; NSATZ=13.45; NSZ=10.09	N S T Z

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Table S11d. Areas definition for each node in Phaethontimorphae-Aequornithia (1 - 0.1 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	N=45.07; S=41.32	N S
2	N=44.40; NS=12.78	N
3	N=16.17; NA=11.75; A=9.56; EA=8.41; E=8.38	N
4	NEAI=15.41; NEA=10.75; NAI=8.74; N=8.12; NSEAI=7.87	N E A I
5	S=80.01	S
6	STZ=100.00	S T Z
7	STZ=42.28; NSTZ=23.67	S T Z
8	S=61.28	S
9	N=28.68; S=20.91; SU=17.34	N S
10	N=18.07; NSAU=11.04; SAU=10.58; NSU=7.92; NA=6.50	N S A U
11	N=14.53; NSAU=10.02; NSEAU=7.68; NSEAIU=5.79; A=5.53; NSA=5.00; NSAIU=4.89	N S A U
12	NSEAU=10.20; NSAU=9.10; NSEAIU=8.90; NSA=6.65; NSAIU=5.97; NSEA=5.80; NEAI=5.44	N S E A U
13	S=46.45; N=33.06	S N
14	NSTZ=30.00; STZ=25.06	N S T Z
15	NEAI=21.04; NEAIU=12.27; NFEAI=9.63; NEA=9.06	N E A I
16	NEAI=25.18; NEA=16.02; NAI=11.72	N E A I
17	NEAI=17.30; NEAIU=13.72; NEA=9.18; NFEAI=7.88; NFEAIU=7.11	N E A I
18	NFEAIU=16.56; NSFEAIU=15.20; NEAIU=7.14; SFEAIU=6.90; NSEAIU=6.52	N S F E A I U
19	A=29.68; N=27.73	A N
20	A=31.92; N=29.23	A N
21	A=31.95; N=29.50	A N
22	A=31.22; N=30.64	A N
23	N=32.03; A=30.28	N A
24	NEAI=15.02; NEA=12.12; EAI=8.59; EA=8.32; NAI=8.20	N E A I
25	N=34.55; A=24.10	N
26	F=11.44; NFEAIU=10.50; E=7.94; NEAIU=7.84; NFEAU=6.28; NFEAI=5.47	N F E A
27	F=100.00	F
28	NFEAIU=15.88; F=11.35; NFEAI=10.69; NFEAU=10.13; FE=9.39	N F E A I U
29	N=23.33; A=19.86; E=17.56	N
30	NEA=15.01; NEAI=12.89; NA=11.95; N=11.09	N E A
31	N=23.07; NA=13.95; E=11.81; EA=10.06	N
32	N=33.27; A=29.48	N A
33	N=35.51; A=31.12	N A
34	NSTZ=20.30; NSATZ=12.24; SETZ=8.76; NSZ=8.14; NSETZ=7.50	N S T Z
35	NSTZ=19.12; NSATZ=11.07; SETZ=8.23; NSETZ=8.00; SATZ=7.45	N S T Z
36	NSATZ=10.10; NSETZ=7.93; NSTZ=7.82; NSEATZ=6.33; NSITZ=5.18; NSAITZ=4.95; SEATZ=4.56; NSEITZ=3.56	N S T Z

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Appendix 3.8.12.

Table S12a. Areas definition for each node in Afroaves (1 - 0.5 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=70.41	S
2	E=100.00	N
3	FE=69.25	F E
4	F=100.00	F
5	F=100.00	F
6	F=100.00	F
7	FE=61.21	F E
8	FE=86.88	F E
9	NFE=100.00	N F E
10	FA=100.00	F A
11	NFE=78.73	N F E
12	NE=33.90; E=28.06	E N
13	E=44.67; NE=25.70	E N
14	FE=69.06	F E
15	E=100.00	E
16	E=100.00	E
17	FEM=100.00	F E M
18	FE=100.00	F E
19	F=100.00	F
20	FEA=32.07; FEAI= 28.70	F E A I
21	E=83.19	E
22	E=67.92	E
23	S=100.00	S
24	FEAI=100.00	F E A I
25	E=48.16; FE=34.45	E F
26	FE=47.28; F=28.85	F E
27	FEAI=80.14	F E A I
28	FEAI=51.28	F E A I
29	E=87.83	E
30	E=100.00	E
31	E=66.62	E
32	FM=100.00	F M
33	FEM=84.98	F E M
34	E=100.00	E
35	E=100.00	E
36	FEAI=38.58; FEA=28.01	F E A I
37	E=100.00	E
38	N=69.93	N
39	NE=48.28; E=34.92	N E
40	NEA=28.46; E=24.11	E N A
41	NE=46.38; E=22.49	N E
42	E=71.24	E
43	E=100.00	E
44	E=100.00	E
45	E=100.00	E
46	E=100.00	E
47	E=100.00	E
48	E=100.00	E
49	E=73.18	E
50	FE=29.06; E=25.77	E F

3. Paleobiogeographic history

Table S12b. Areas definition for each node in Afroaves (1 - 0.25 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=82.91	S
2	E=100.00	N
3	FE=70.06	F E
4	F=100.00	F
5	F=100.00	F
6	F=100.00	F
7	FE=64.61	F E
8	FE=87.23	F E
9	NFE=100.00	N F E
10	FA=100.00	F A
11	NFE=75.49	N F E
12	NE=33.04; NFE=31.65	E N F
13	E=31.92; NE=23.69	E N
14	FE=61.99	F E
15	E=100.00	E
16	E=100.00	E
17	FEM=100.00	F E M
18	FE=100.00	F E
19	F=100.00	F
20	FEA=30.84; FEAI=30.05	F E A I
21	E=78.68	E
22	E=63.25	E
23	S=100.00	S
24	FEAI=100.00	F E A I
25	E=48.24; FE=30.46	E F
26	FE=38.45; F=29.58	F E
27	FEAI=81.23	F E A I
28	FEAI=51.17	F E A I
29	E=87.09	E
30	E=100.00	E
31	E=64.93	E
32	FM=100.00	F M
33	FEM=100.00	F E M
34	E=100.00	E
35	E=100.00	E
36	FEAI=42.48; FEA=29.08	F E A I
37	E=100.00	E
38	N=73.34	N
39	NE=52.90	N E
40	NEA=34.67; E=22.64	E N A
41	NE=45.66; NEA=27.72	N E A
42	E=60.05	E
43	E=100.00	E
44	E=100.00	E
45	E=100.00	E
46	E=100.00	E
47	E=100.00	E
48	E=100.00	E
49	E=56.84	E
50	FE=28.21; NFE=25.89	F E N

3. Paleobiogeographic history

Table S12c. Areas definition for each node in Afroaves (1 - 0.5 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	N=58.60	N
2	E=100.00	N
3	F=47.42; FE=45.24	F E
4	F=100.00	F
5	F=100.00	F
6	F=100.00	F
7	F=56.88	F
8	FE=100.00	F E
9	NFE=100.00	N F E
10	FA=100.00	F A
11	NFE=68.30	N F E
12	E=54.13	E
13	E=69.33	E
14	FE=60.20	F E
15	E=100.00	E
16	E=100.00	E
17	FEM=100.00	F E M
18	FE=100.00	F E
19	F=100.00	F
20	FEA=34.00; FEAI=27.09	F E A I
21	E=100.00	E
22	E=76.92	E
23	S=100.00	S
24	FEAI=100.00	F E A I
25	E=54.22	E F
26	FE=32.78; F=31.12	F E
27	FEAI=77.63	F E A I
28	FEAI=49.40; FEA=24.02	F E A I
29	E=84.95	E
30	E=100.00	E
31	E=63.16	E
32	FM=100.00	F M
33	FEM=76.57	F E M
34	E=100.00	E
35	E=100.00	E
36	FEAI=35.49; FEA=30.67	F E A I
37	E=100.00	E
38	N=58.79	N
39	E=44.72; NE=29.86	E N
40	E=33.61; NEA=18.19	E
41	NE=33.04; E=32.00	N E
42	E=71.42	E
43	E=100.00	E
44	E=100.00	E
45	E=100.00	E
46	E=100.00	E
47	E=100.00	E
48	E=100.00	E
49	E=100.00	E
50	E=34.56; FE=28.93	E F

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Table S12d. Areas definition for each node in Afroaves (1 - 0.1 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	N=73.53	N
2	E=100.00	N
3	F=67.17	F
4	F=100.00	F
5	F=100.00	F
6	F=100.00	F
7	F=66.17	F
8	FE=100.00	F E
9	NFE=100.00	N F E
10	FA=100.00	F A
11	NFE=63.88	N F E
12	E=35.29; NFE=17.08	E
13	E=45.49; NFE=13.51	E
14	E=63.27	F E
15	E=100.00	E
16	E=100.00	E
17	FEM=100.00	F E M
18	FE=100.00	F E
19	F=100.00	F
20	FEAI=28.87; FEA=27.88	F E A I
21	E=82.32	E
22	E=70.04	E
23	S=100.00	S
24	FEAI=100.00	F E A I
25	E=48.79; F=42.41	E F
26	F=45.62; E=39.94	F E
27	FEAI=79.83	F E A I
28	FEAI=51.72	F E A I
29	E=81.43	E
30	E=100.00	E
31	E=57.49	E
32	FM=100.00	F M
33	FEM=74.19	F E M
34	E=100.00	E
35	E=100.00	E
36	FEAI=47.11; FEA=31.58	F E A I
37	E=100.00	E
38	N=78.11	N
39	E=29.48; N=21.84	E
40	E=23.77; NEA=22.01	E
41	NEA=25.54; NE=19.58; E=19.48	E N A
42	E=49.80; EA=20.78	E
43	E=100.00	E
44	E=100.00	E
45	E=100.00	E
46	E=100.00	E
47	E=100.00	E
48	E=100.00	E
49	E=85.92	E
50	FE=25.97; NFE=17.94; E=12.63	E F

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Appendix 3.8.13.

Table S13a. Areas definition for each node in Australaves (1 - 0.5 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=57.33	S
2	S=78.38	S
3	S=76.62	S
4	ST=100.00	S T
5	UZ=100.00	U Z
6	U=70.86	U
7	U=77.06	U
8	UZ=100.00	U Z
9	U=68.71	U
10	STU=42.01; SU=16.91	S T U
11	STU=28.93; SU=11.13; STZ=10.92	S T U

Table S13b. Areas definition for each node in Australaves (1 - 0.25 - 0.1 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=52.84	S
2	S=80.02	S
3	S=80.56	S
4	ST=100.00	S T
5	UZ=100.00	U Z
6	U=83.05	U
7	U=100.00	U
8	UZ=100.00	U Z
9	U=72.67	U
10	STU=33.97; SU=18.88	S T U
11	STU=30.22; SU=16.27; NSTU=9.42	S T U

Table S13c. Areas definition for each node in Australaves (1 - 0.5 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=64.29	S
2	S=81.61	S
3	S=80.22	S
4	ST=100.00	S T
5	UZ=100.00	U Z
6	U=72.08	U
7	U=76.85	U
8	UZ=100.00	U Z
9	U=76.45	U
10	STU=56.20	S T U
11	STU=43.84; STZ=15.65	S T U

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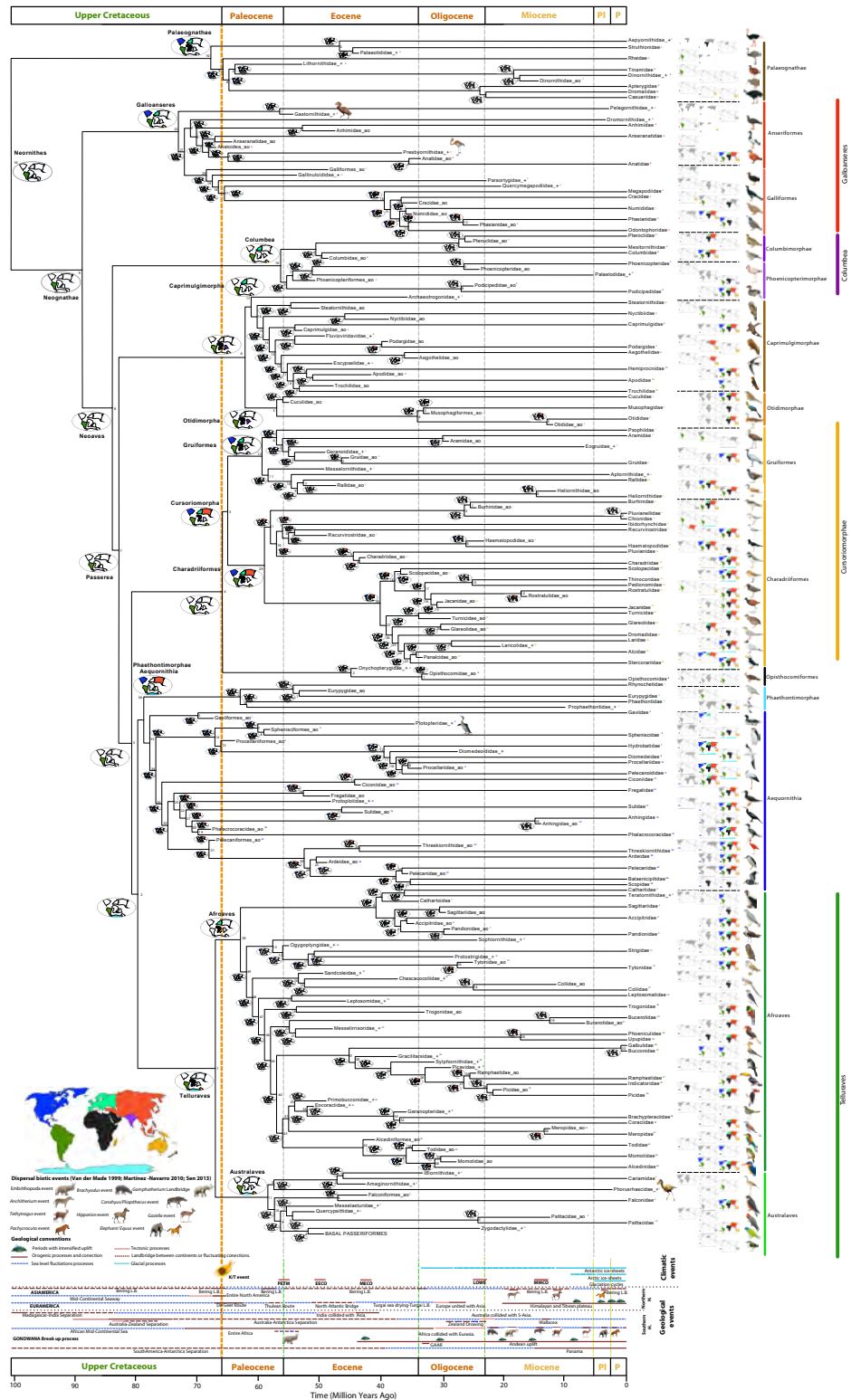
Table S13d. Areas definition for each node in Australaves (1 - 0.1 - 0 Model). **(N)** North and Central America; **(S)** South America; **(E)** Europe; **(A)** Asia; **(I)** India; **(F)** Africa; **(U)** Australia; **(T)** Antarctica; **(M)** Madagascar; **(Z)** Zealand.

Node	Probability of combinations % (until 50%)	Defined areas
1	S=77.28	S
2	S=100.00	S
3	S=100.00	S
4	ST=100.00	S T
5	UZ=100.00	U Z
6	U=100.00	U
7	U=100.00	U
8	UZ=100.00	U Z
9	U=87.32	U
10	STU=69.02	S T U
11	STU=58.36	S T U



3. *Paleobiogeographic history*

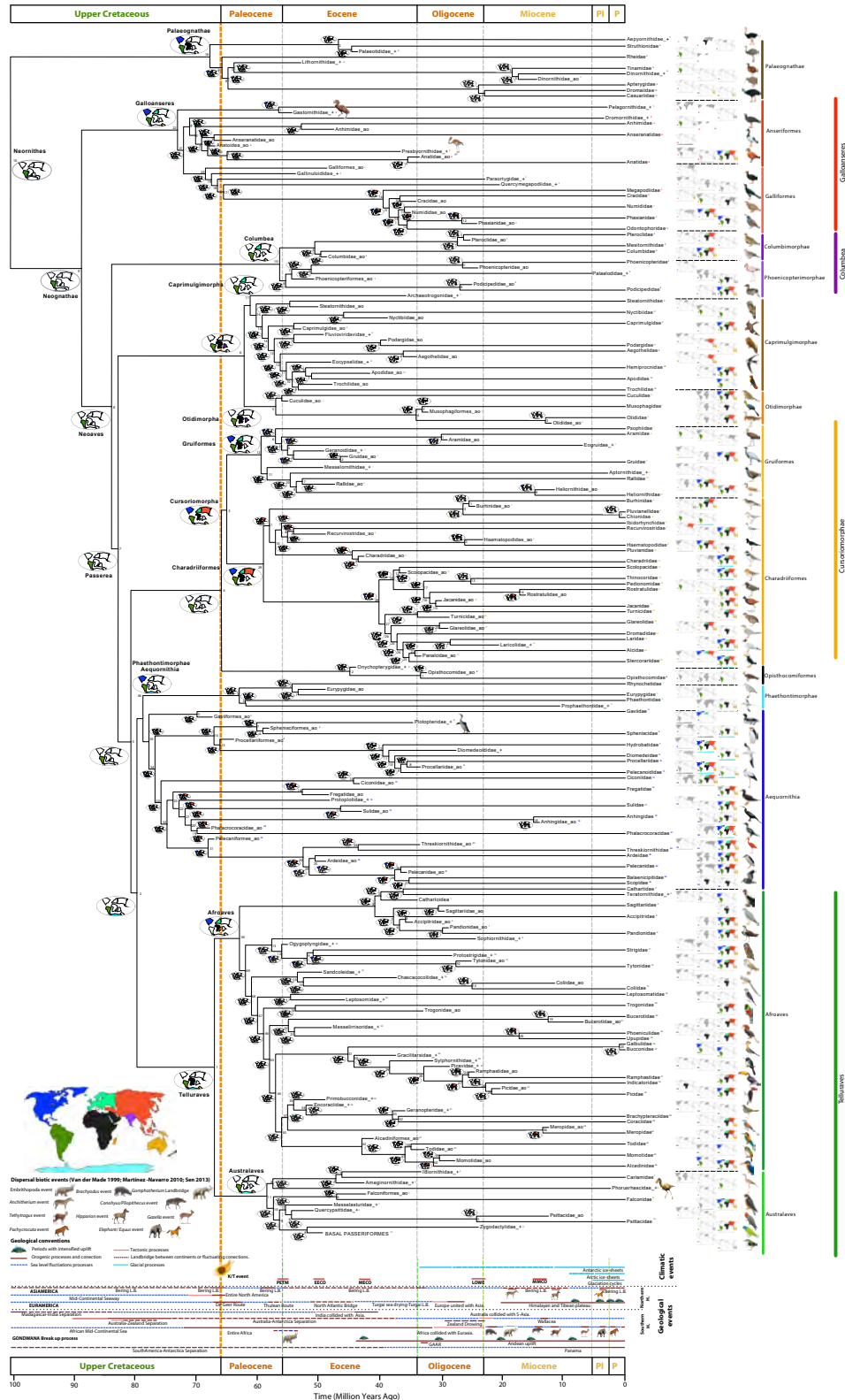




Appendix 3.8.14. Figure S1. Paleobiogeographical reconstruction according with the 1-0.5-0.1 Model using Lagrange (DEC). The inferred ancestral area(s) with the highest relative likelihood (in the nodes) (see Tables S3- S13 for details.) the maps indicate the geographical distribution of families based in the fossil record and their current distribution.

3. Paleobiogeographic history

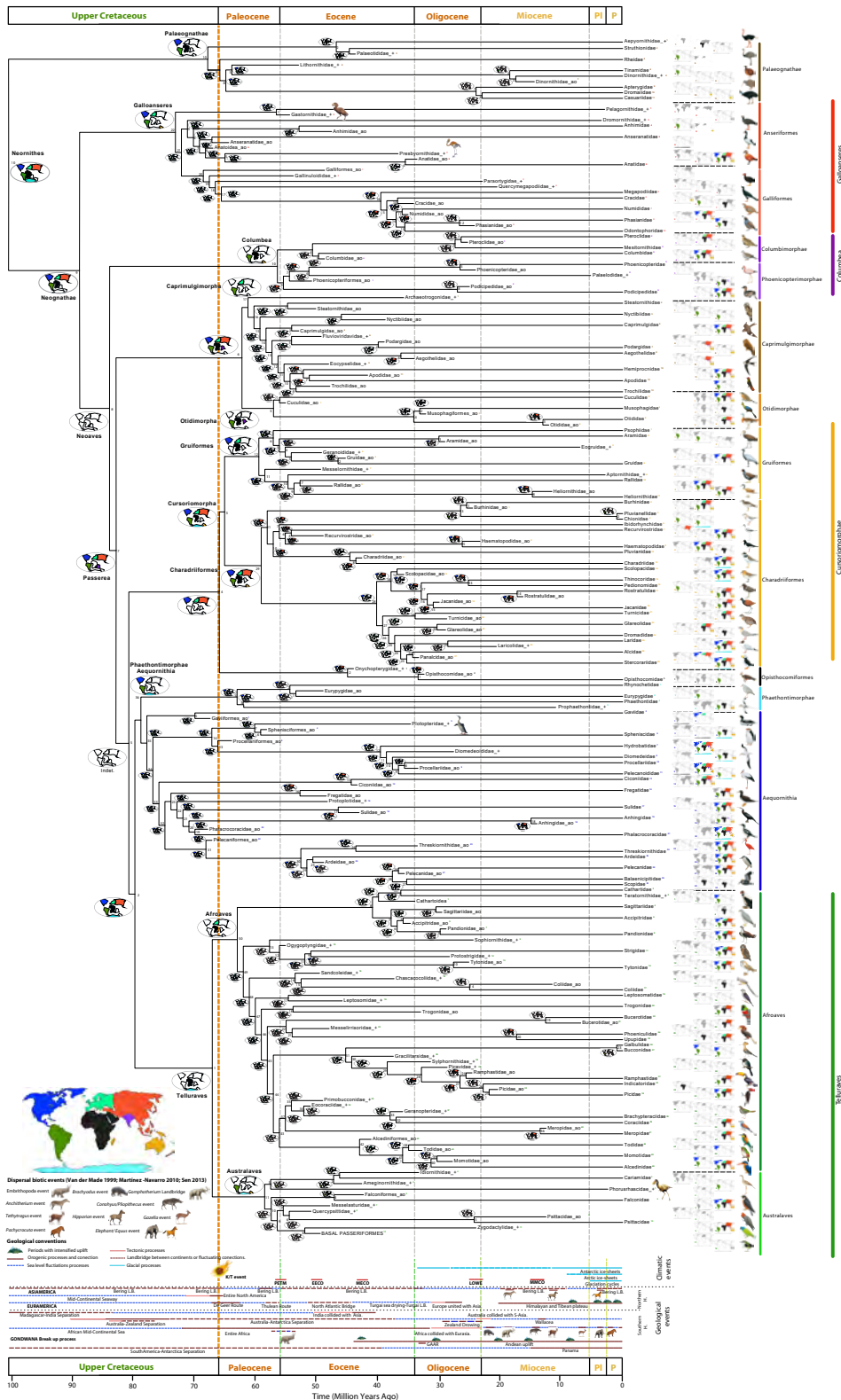
3. Paleobiogeographic history



Appendix 3.8.15. Figure S2. Paleobiogeographical reconstruction according with the 1-0.25-0.1 Model using Lagrange (DEC). The inferred ancestral area(s) with the highest relative likelihood (in the nodes) (see Tables S3- S13 for details.) the maps indicate the geographical distribution of families based in the fossil record and their current distribution.

3. Paleobiogeographic history

3. *Paleobiogeographic history*

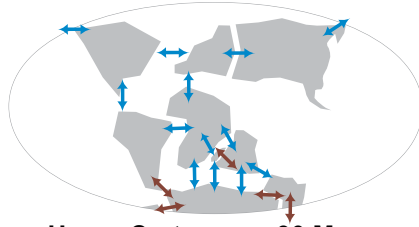


Appendix 3.8.16. Figure S3. Paleobiogeographical reconstruction according with the 1-0.5-0 Model using Lagrange (DEC). The inferred ancestral area(s) with the highest relative likelihood (in the nodes) (see Tables S3- S13 for details.) the maps indicate the geographical distribution of families based in the fossil record and their current distribution.

3. Paleobiogeographic history

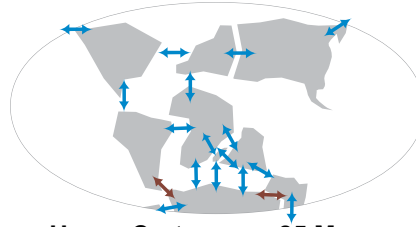
3. Paleobiogeographic history

3. Paleobiogeographic history



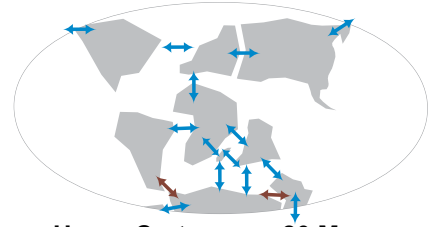
**Upper Cretaceous 90 M.y.a
(Turonian-Coniacian)**

Gondwana fragmentation ⁽¹⁻¹³⁾, I+M⁽¹⁴⁾, I/T^(6,14)
S+T^(1-4,10), S/F^(2,5), S/N^(2,6-8), U++T+Z⁽¹⁵⁻¹⁸⁾, N/A^(2,3)
E/A^(2,9), N/A^(2,3), F/T⁽¹⁴⁾, F/E^(2,10)



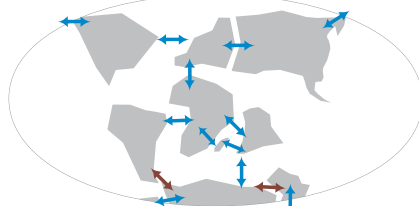
**Upper Cretaceous 85 M.y.a
(Santonian)**

Gondwana fragmentation ⁽¹⁻¹³⁾, U+T^(1,16), U/Z^(1,19-22), I/M^(14,23-29), T/Z^(2,18-22)



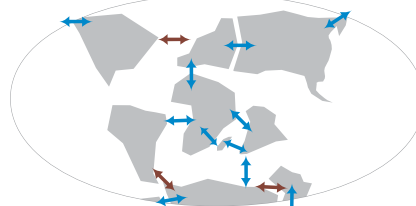
**Upper Cretaceous 80 M.y.a
(Campanian)**

Gondwana fragmentation ⁽¹⁻¹³⁾, N/S^(2,6,12), IM/T⁽¹⁴⁾, I/M^(14,26,28), F/T^(2,10,14)



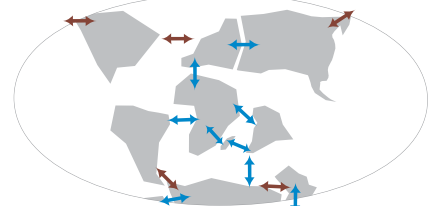
**Upper Cretaceous 75 M.y.a
(Maastrichtian)**

Gondwana fragmentation ⁽¹⁻¹³⁾
I/M⁽²⁵⁻²⁹⁾, F/T^(2,10,14,30)



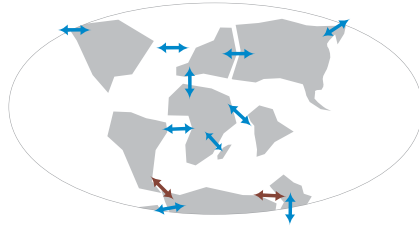
**Upper Cretaceous 69 M.y.a
(Maastrichtian)**

I/T⁽²⁶⁾, F/I⁽²⁵⁾, N+E⁽³¹⁾



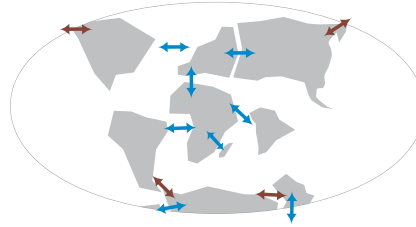
**Upper Cretaceous 66 M.y.a
(K/Pg Boundary)**

N+A^(31,32), E/A^(32,33)



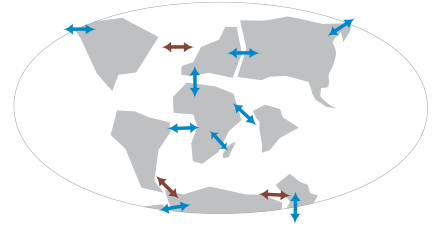
**Middle Paleocene 60 M.y.a
(Selandian)**

S+T⁽¹⁾, F/I^(14,28), N/E^(31,32), N/A^(31,32), E/A^(33,34)



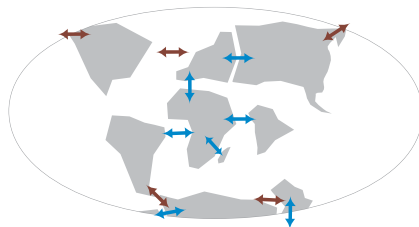
**Upper Paleocene 58 M.y.a
(Thanetian)**

N+A⁽³¹⁾



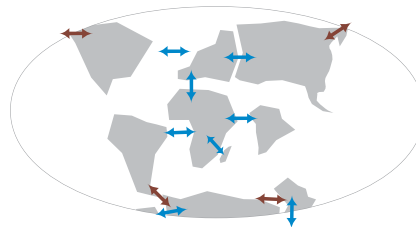
**Upper Paleocene 57 M.y.a
(Thanetian)**

E/A^(33,34), N/A⁽³¹⁾, N/E⁽³¹⁾



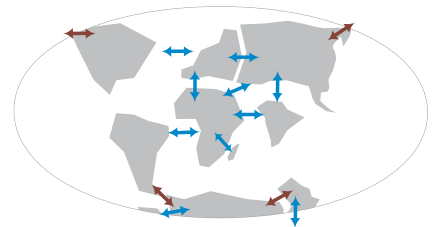
**Upper Paleocene 56 M.y.a
(P/Eo Boundary)**

E/A^(33,34), N+A^(35,36)



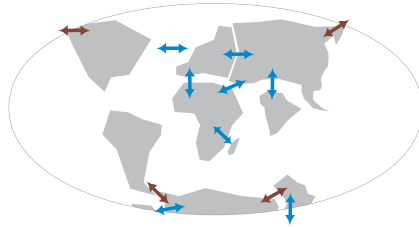
**Lower Eocene 55 M.y.a
(Ypresian)**

E/A^(33,34), E/N⁽³¹⁾



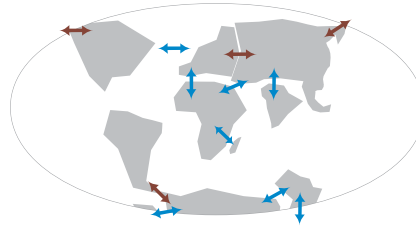
**Lower Eocene 50 M.y.a
(Ypresian)**

E/A^(33,34), F/A^(10,37), F/I⁽¹⁴⁾, I/A^(14,28,29)



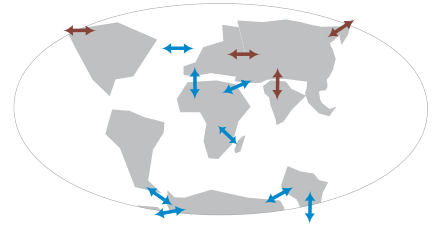
**Lower Eocene 48 M.y.a
(Ypresian)**

S/F⁽⁹⁾, E/A^(33,34), U+T^(15,16, 20, 30,38)



**Middle Eocene 40 M.y.a
(Bartonian)**

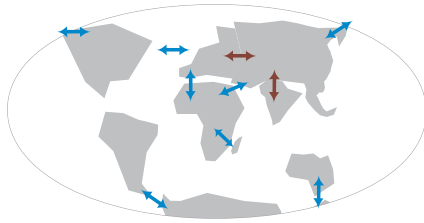
E+A⁽³²⁻³⁴⁾, U/T^(15,16, 20, 30)



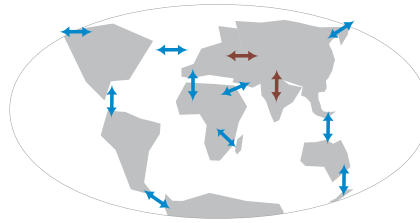
**Upper Eocene 34 M.y.a
(Eo/Og Boundary)**

E++A^(3,32-34), I+A⁽³⁹⁾, S/T^(30,38,40)

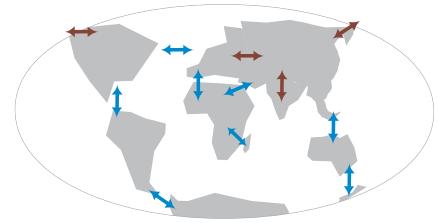
3. Paleobiogeographic history



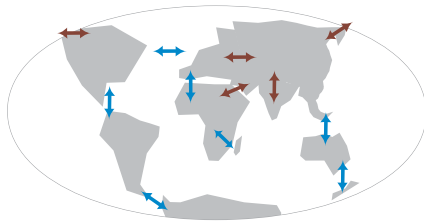
**Lower Oligocene 30 M.y.a
(Rupelian)**
N/A⁽³⁶⁾, U/T^(16,20)



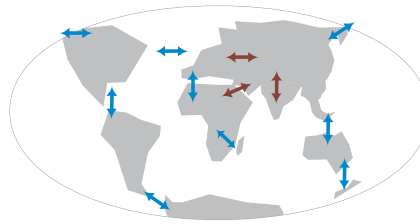
**Upper Oligocene 25 M.y.a
(Chattian)**
U/A^(16,20), S/N^(41,42)



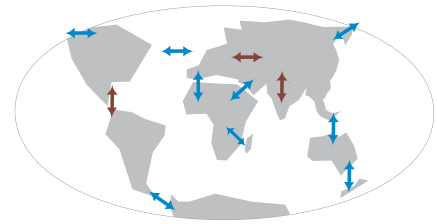
**Lower Miocene 20 M.y.a
(Burdigalian)**
N+A^(43,44)



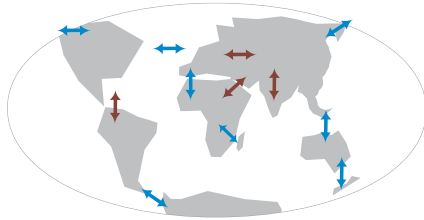
**Lower Miocene 18 M.y.a
(Burdigalian)**
N+A^(43,44), A+F^(37,43-45)



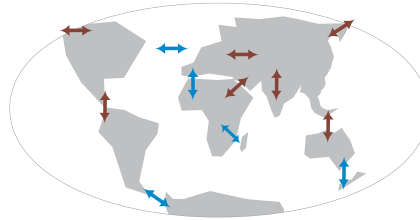
**Lower Miocene 17 M.y.a
(Burdigalian)**
N/A^(43,44)



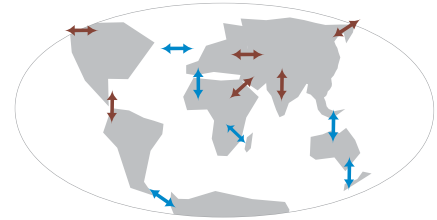
**Lower Miocene 15 M.y.a
(Langhian)**
F/A^(44,45), S++N⁽⁵⁰⁻⁵⁴⁾



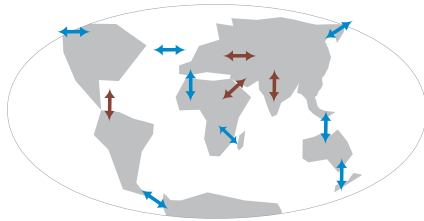
**Middle Miocene 13.8 M.y.a
(Serravallian)**
F+A^(43,45)



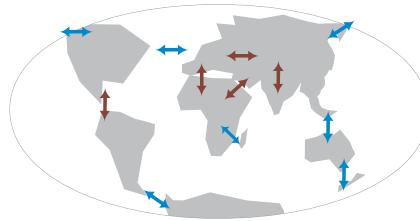
**Middle Miocene 12 M.y.a
(Serravallian)**
U+A^(3,16), N+A^(43,44)



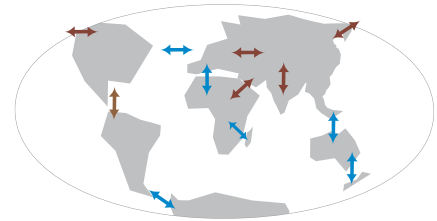
**Upper Miocene 10 M.y.a
(Tortonian)**
N+A^(43,44)



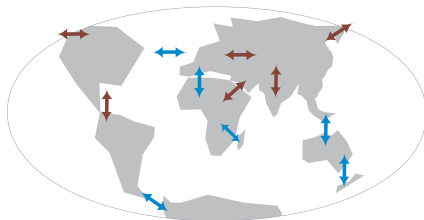
**Upper Miocene 7.5 M.y.a
(Tortonian)**
N/A^(43,44), U/A^(3,16)



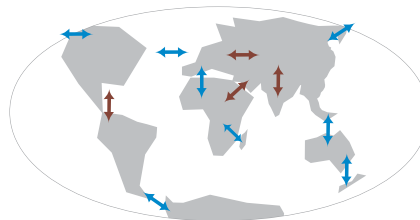
**Upper Miocene 5.9 M.y.a
(Messinian)**
F+E^(43,46)



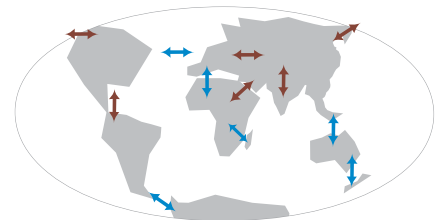
**Lower Pliocene 4.8 M.y.a
(Zanclean)**
N+A⁽⁴⁷⁻⁴⁹⁾, F/E^(43,46)



**Lower Pliocene 3.5 M.y.a
(Zanclean)**
S++N⁽⁵⁰⁻⁵³⁾



**Upper Pliocene 3 M.y.a
(Piacenzian)**
N/A⁽⁴⁷⁻⁴⁹⁾



**Lower Pleistocene 2 M.y.a
(Gelasian)**
N+A^(32,47-49)

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Appendix 3.8.18. Figure S5. 30 geological periods considered for the paleobiogeographical analysis: (++) complete connection between landmasses; (+) Partial connection between landmasses by bridges or Islands (stepping stones); (/) separations between landmasses by seaway with less than 2000 km of distance each other; (//) complete separation between landmasses with more than 2000 km of distance each other.

(N) North and Central America; (S) South America; (E) Europe; (A) Asia; (I) India; (F) Africa; (U) Australian; (T) Antarctica; (M) Madagascar; (Z) Zealand.

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Global processes: [1-8]; *Gondwana*: [2, 6, 9-14]; *Australia (U)*: [15-20]; *New Zealand (Z)*: [15, 18, 21, 22]; *Madagascar (M)*: [23-26]; *India (I)*: [14, 17, 23, 27-29, 39]; *Antarctica (T)*: [18, 19, 30, 38]; *Africa (F)*: [10, 37, 45, 46]; *South America (S)*: [40, 41, 42, 50-54]; *North America (N)*: [31, 32, 35, 36, 41-44, 47-54]; *Europe (E)*: [31, 33, 34, 44, 46,]; *Asia (A)*: [32-37, 43-45, 47-49].

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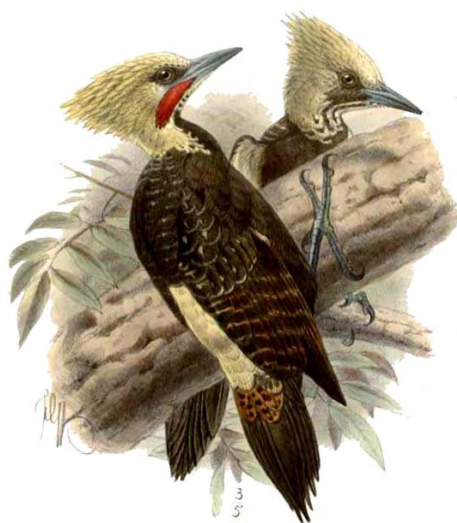
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4

Phylogeny and biome occupancy





A phylogenetic perspective on bird occupation and adaption: Galliformes and Falconiformes as contrasting cases

4

“...By far, the most remarkable feature in the natural history of this archipelago... is that the different islands to a considerable extent are inhabited by a different set of beings.”

Charles Darwin, *the Voyage of the Beagle* (1839)

“The extreme clarity of the desert light is equalled by the extreme individuation of desert life forms...”

Edward Abbey, *Desert solitaire* (1968)

ABSTRACT

The influence of historical climatic and geological events on evolutionary dynamics of birds at broad scale has been studied under different points of view. However, the integration of diverse evolutionary hypotheses related with their ecological specialization and cladogenesis are still incomplete. In this sense, biomes are key ecological units that integrate climatic variables, current landscapes and particular histories linked to geologic processes, which configures specific biotas in constant evolution. These features consolidate the biomes as “evolutionary scenarios” with their own diversification dynamics. According to this, what environmental factors

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would be determinant in the colonization of the different biomes through time by clades originating in other biomes? We assess ancestral biome occupancy under the phylogenetic niche conservatism concept, which will allow us to analyse geographic distribution patterns and adaptation to different climate regimes. These aspects are fundamental to understand the underlying dynamic of subsequent diversification in each biome. In this work, we reconstructed the biome colonization history of two clades of birds: Galliformes and Falconiformes. These groups show different trophic characteristics, which allowed us to assess the effect of diet in their evolutionary patterns. Overall, our findings for both groups are broadly consistent with a scenario of phylogenetic biome conservatism and highlight the significant importance of global climate changes during the Miocene in the adaptation and evolution of climate niche in both groups. Finally, the historical dynamics of dry and seasonal biomes such as tropical deciduous woodlands and savannas have a preponderant role in the diversification of these groups.

Keywords: Ancestral Biome occupancy, Cenozoic, Climate niche evolution, Macroevolution, Neogene, Phylogenetics.

4.2. INTRODUCTION

Biomes have acquired a broad relevance as analytical units in macroecological and macroevolutionary studies on the connection between climatic gradients and vertebrate diversity gradients (Hawkins et al. 2003; Pennington et al. 2004a; Crisp 2006; Crisp et al. 2009; Jetz and Fine 2012; Cantalapiedra et al. 2014). The biome concept integrates the biotic assemblage and a varied series of abiotic conditions, mainly based on mean annual values of different climatic variables (Walter 1970; Whittaker 1975; Strahler and Strahler 1987). The confluence of these factors configures a determinate climate regime, which favours a specific plant physiognomy (Holdridge 1967; Walter 1970; Whittaker 1975; Woodward et al. 2004; Donoghue 2008; Donoghue and Edwards 2014). The particular features of each biome and their own geological and climatic history may favour a novel understanding of the relationship between diverse taxa including historical biome dynamics and the configuration of evolutionary processes, patterns of diversification and colonization of new environments at global scale (Jansson 2003; Guerrero et al. 2013; Giarla and

Jansa 2014; Davies et al. 2011; Cantalapiedra et al. 2011; Toussaint et al. 2012; Cantalapiedra et al. 2014).

Biomes differ in origin age and have suffered many geographic fluctuations during the Cenozoic (Potts and Behrensmeyer 1992; Flower and Kennett 1994; Senut et al. 2009; Jaramillo et al. 2010) due to their dependency on globally changing climates. These historical patterns can be inferred using techniques that use global climate models and paleobotanical data (Valdes 2000; Kohfeld and Harrison 2000; Harrison and Prentice 2003; Salzmann et al. 2008). In accordance with such models, during the Neogene the biomes experimented changes consistent with a global cooling and drying trend (Zachos et al. 2001; Salzmann et al. 2008; Pound et al. 2012). In this context, different biomes have exhibited different geographic dynamics (contraction, fragmentation-expansion and generation of new environments), creating diverse evolutionary scenarios (Vrba 1992, 1995; Hernández Fernández and Vrba 2005; Jetz and Fine 2012; Donoghue and Edwards 2014).

According to the environmental niche conservatism hypothesis, the species tend to preserve and share ancestral adaptive and ecological traits adjusted by phylogenetic constraints (Peterson et al. 1999; Wiens 2004; Wiens et al. 2010). Specific environmental conditions might promote the development of physiological traits to cope adverse conditions in many climate regimes that requires highly specialized functional features and requirements (Janzen 1967; Ghalambor et al. 2006). Conversely, a high versatility level in relation to resources and climatic conditions could *a priori* enable a prominent capacity to colonize and occupy diverse habitat types (Jocque et al. 2010; Salisbury et al. 2012; Pigot and Tobias 2013, 2015). This could explain how, despite phylogenetic niche conservatism, many clades had succeed in the colonization of new available habitats as new biomes evolved (Guerrero et al. 2013). In many cases, paleoclimatic shifts might have promoted environmental flexibility by expansion of the climatic tolerance (Guerrero et al. 2013; Jara-Arancio et al. 2014). This process depends on genetic variation of species populations, which allows them to broaden their climatic niche and to colonize new environments.

The integration of niche conservatism theory and the biome concept generates a macroevolutionary context where the biome conservatism might has an important role for explaining the global latitudinal gradient of species richness (Crisp et al.

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2009). This conceptual framework also constitutes a key to recognize the mode and tempo of climatic niche evolution by developing of adaptations in the phylogenetic history of taxa to invade a novel environment (Crisp et al. 2009; Guerrero et al. 2013; Jara-Arancio et al. 2014; Donoghue and Edwards 2014). The process of biome colonization may provide valuable information about possible morphophysiological constraints or the ecological and climatic versatility that would permit adaptation to adverse biomes such as the desert or tundra.

Birds are good indicators for macroevolutionary and macroecological studies due to their well-known biogeography, great diversity and relative well-established phylogenies (Jetz et al. 2012; Jarvis et al. 2014). In this study, we analysed the pattern of biome occupancy and their conservatism in Galliformes and Falconiformes in relation with past climatic changes and geological processes that could have influenced their evolution and adaptation to specific climatic regimes. Both taxa present broad global distributions and inhabit all the world's biomes. In addition, these groups have a distinctive ecology occupying different trophic positions, both herbivorous and faunivorous. Finally, our analysis of biome occupancy under phylogenetic perspective in these bird groups allows integrating the influence of diverse climatic and geological events with the biomes colonization processes, which allow us to evaluate the biome conservatism tendencies and understand the importance of the different biomes in the diversification processes in both taxa.

4.3. MATERIALS AND METHODS

4.3.1. *Studied taxa and phylogenetic information*

The order Galliformes (landfowl and allies) holds 289 extant species, all of them with predominantly herbivorous diet (Del Hoyo et al. 1992). In addition to their environmental variability, Galliformes exhibit a broad body size range, from the relatively small common quail (*Coturnix coturnix*, near 35g) to the wild turkey (*Meleagris gallopavo*, about 5kg). The phylogenetic relationships of the Galliformes are among the best known within birds. Phylogenetic hypothesis for the group was initially based on morphological data and has been updated recently with the implementation of molecular techniques (Eo et al. 2009; Kimball et al. 2011; Hugall and Stuart-Fox 2012; Wang et al. 2013; Stein et al. 2015). This monophyletic group

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is divided in five families: Megapodidae (brush-turkeys and scrubfowls), Cracidae (curassows and guans), Numididae (guineafowls), Odontophoridae (New World quails) and Phasianidae (pheasants, Old World quails, grouses and turkeys). Nevertheless, there is no complete phylogeny at the species level for this order yet. For this reason we built an informal dated supertree that integrates 77.8 % of the species (225 species) taking into account the most complete calibrated phylogenies published to this date (Hugall and Stuart-Fox 2012; Stein 2013; Wang et al. 2013; Stein et al. 2015). For taxonomic consistency, the nomenclature for the consensus tree was adapted according to Del Hoyo and Collar (2014).











The order Falconiformes (falcons and allies) includes 66 species classified within the family Falconidae (Fuchs et al. 2012; Del Hoyo and Collar 2014; Fuchs et al. 2015). Overall, falcons are faunivorous with a body size spectrum from small species such as black-thighed falconet (*Microhierax fringillarius*, 35 g) to the gyr falcon (*Falco rusticolus*, 1.7kg) (Ferguson-Lees and Christie 2001). Ecologically, falcons have a great variety of habitat preferences that includes forest, savanna, desert and steppes; many species show a wide spectrum of environmental occupation as in the case of peregrine falcon (*Falco peregrinus*) with a worldwide distribution. Considering their phylogenetic relationships, two subfamilies are well established: Herpetotherinae (laughing and forestal falcons) and Falconinae (caracaras, falconets, falcons and kestrels). We employed the most complete falcon phylogeny published recently by Fuchs et al. (2015), which includes all the species. To conserve the taxonomic consistence, we used Del Hoyo and Collar (2014).

4.3.2. Biomes selection and occupation data

We selected the biome classification system developed by Walter (1970) and modified by Hernández Fernández (2001), which establishes ten biomes considering the annual relative distribution of temperature and precipitation (Table 1). Paleoclimatic studies reveal diverse variation in the age and spatial dynamic of the biomes (Pennington et al. 2004a; Jetz and Fine 2012). The oldest biomes —such as evergreen tropical rainforest— have been reported since the Cretaceous and Paleocene (Davis et al. 2005; Jaramillo et al. 2010; Jaramillo 2012; Jaramillo and Cárdenas 2013). Successively during the Eocene, with the climatic fluctuations of rainforest appeared areas of tropical deciduous woodland and savanna (Bredenkamp et al. 2002; Jacobs 2004; Pennington et al. 2004a; Jaramillo and Cárdenas 2013),

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Table 1. Biomes structure and age (f: forest environments; o: open environments)

Biome	Biome type	Age of origin	References
Evergreen tropical rainforest (I)	 (f)	Late Cretaceous – Paleocene	(Jaramillo et al. 2010; Jaramillo 2012; Davis et al. 2005)
Tropical deciduous woodland (II)	 (f)	Early Eocene (small areas) Early Oligocene (Cover large areas)	(Pennington et al. 2004; Jacobs 2004; Werneck et al. 2011)
Savanna (II/III)	 (o)	Early Eocene (small areas) Late Miocene (cover large areas)	(Jacobs 2004; Pennington et al. 2004; Beerling and Osborne 2006)
Subtropical desert (III)	 (o)	Early Oligocene (small areas) Pliocene (cover large areas)	(Shmida 1985; Senut et al. 2009; Guerrero et al. 2013)
Sclerophyllous woodland-Shrubland (IV)	 (f)	Late Miocene (small areas) Plio-Pleistocene (cover large areas)	(Hernandez Fernandez et al. 2007; Buerki et al. 2012; Pennington et al. 2004)
Temperate evergreen forest (V)	 (f)	Early Eocene	(Markgraf et al. 1995; Fine and Ree 2006; DeVore and Pigg 2013)
Broadleaf deciduous forest (VI)	 (f)	Early Eocene	(Markgraf et al. 1995; Fine and Ree 2006; DeVore and Pigg 2013)
Steppe to cold desert (VII)	 (o)	Early Miocene (small areas) Plio-Pleistocene (cover large areas)	(Axelrod 1985; Janis 1993; Zimov et al. 1995; Franzke et al. 2004; Wang 2004; Kahlke 2014)
Boreal coniferous forest (VIII)	 (f)	Middle-Late Miocene	(DeVore and Pigg 2013; Fine and Ree 2006; Pound et al. 2011)
Tundra (IX)	 (o)	Plio-Pleistocene	(Zimov et al. 1995; Kahlke 2014)

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which extended broadly during the Oligocene and Late Miocene respectively (Pennington et al. 2004b; Edwards et al. 2010). Likewise, during the Eocene emerged temperate evergreen forest and broadleaf deciduous forest biomes in high-latitude zones (Axelrod 1966; Markgraf et al. 1995; DeVore and Pigg 2013). During the middle-late Miocene, after the Mid-Miocene Climate Optimum, the drop of temperature gradients triggered the increase of aridity conditions (Zachos et al. 2001). These factors promoted the origin of boreal coniferous forest in highest latitudes (Wolfe 1985; Pound et al. 2011; Popova et al. 2012). Meanwhile, other more open biomes such as savannas, steppes and deserts began to expand in the drier and arid areas (Axelrod 1985; Bredenkamp et al. 2002; van Dam 2006; Byrne et al. 2008; Senut et al. 2009; Guerrero et al. 2013). Along the Pliocene and Pleistocene diverse extreme climatic events caused phases of icehouse and subsequent glaciations, which propitiated the emergency of biomes such as sclerophyllous woodland-shrubland (Hernandez Fernandez et al. 2007; Buerki et al. 2012) and tundra polarwards (Wolfe 1985; Zimov et al. 1995; Hewitt 2003). Moreover, this period implied the prominent expansion of steppes in high latitudes (Franzke et al. 2004; Kahlke 2014) and deserts in subtropical latitudes (Bobe 2006; Senut et al. 2009) with the opposite effect of area contractions of tropical and wet biomes (Hooghiemstra and Van der Hammen 2004; Jaramillo and Cárdenas 2013; Raes et al. 2014).

The biome occupation of each species was determined following the methodology developed by Hernández Fernández (2001). According with the geographic information for the distribution of each species, we codified the presence or absence of species in each biome considering the relative size of its geographical range. If 15% or more of the species geographical range is situated within a specific biome, the species is considered to occupy that biome. For the case of biomes with relative small areas respect to the species geographical range, we also recorded the presence of species when the species inhabits 50% or more of one climatic dominion. The species with presence in mountain environments were registered as presence in correspondence with the analogous biome considering the altitudinal climatic gradient.

4.3.3. *Ancestral biome reconstruction*

For reconstructing ancestral biome occupations we modelled the occurrence of species in the ten biomes along the evolutionary history of Galliformes and

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Falconiformes using a phylogenetic approach. The ancestral biome occupation for all lineages was estimated through maximum likelihood analysis of geographic range evolution using the package BioGeoBEARS (BioGeography with Bayesian and Likelihood Evolutionary Analysis) implemented in R (Matzke 2013). This analysis allowed us to model the dynamics of biome occupation in relation to the timing of cladogenesis based on the splitting times of the phylogenetic trees. Although it was originally designed for the study of biogeographic evolution, BioGeoBEARS is an analytic approximation that allows probabilistic inference of ecological characters, biome occupation in our case, integrating different models onto a time-calibrated phylogenetic tree (Batalha-Filho et al. 2014; Alfaro et al. 2015; Buckner et al. 2015; Mendoza et al. 2015; de Medeiros and Lohmann 2015). This tool enabled us to infer the ancestral biome in each node along the phylogeny. BioGeoBEARS estimates maximum likelihood for ancestral states during speciation events modelling the transitions between different states (biomes occupied) along the phylogenetic branches as a function of time. The analyses were conducted using the dispersal-extinction-cladogenesis model (DEC) (Ree and Smith 2008), modified in BioGeoBEARS with the new parameter j (for *jump*) (Matzke 2014a; Matzke 2014b). The analyses took into account the adjustment of the specific parameters for the evolutionary model (d =dispersal and e = extinction) and the novel parameter j , which models the process of founder-event speciation (Matzke 2014a). Due to evolutionary biome dynamic, we configured a BioGeoBEARS supermodel with freedom the parameters of DEC- j analyses, respect to the effect of specific and diverse dispersal capacities within the families that allow differential probabilities of biome colonization by the long-distance mechanisms (Price and Clague 2002; Pigot and Tobias 2015).

Processes of climate change have altered the ecological conditions of the earth over geologic time. This has led to different biomes having particular histories in relation with their origin and processes of geographic fluctuation. Considering this, for the DEC- j analysis we included a “biome existence matrix”, which incorporates information about the availability of each biome along the Cenozoic. In this way, we introduced temporal constraints related to the geological, climatic and ecological history of biomes in the analysis. Likewise, due to the diverse points of view regarding the extent and age of the biomes, the opinion respect of their origin in small areas present more uncertainly and diverse interpretations (Jetz and Fine

2012). Thus, when building the biome availability matrix, we considered origin-age estimates based on robust fossil and geological evidence (Table S1, Appendix 4.8).

We also established a “biomes connection matrix”, which allows the inclusion of changing dispersal probabilities between biomes across the temporal span of the analyses. This was constructed based on climatic and geographical information of biomes in relation to all non-passerine birds (3951 spp) observed occupation (Chapter 1) with near 239 biome combinations (Table S2 in Appendix 4.8). These 239 combinations represent the biologically possible connection between biomes in order to avoid the computational intractability of the analysis with all combinations (1023) (Hernández Fernández and Vrba 2005; Matzke 2013).

The reconstruction process of ancestral biome occupancy combines all the information (living species biome occupation, the tree topology, the availability and the connections among biomes through time) and yields the likelihood values for each biome combinations in each node. BioGeoBEARS output for ten-areas analyses is complex. In order to organize the results and obtain the general patterns of historical biome occupation, we established a criterion based in the selection of the biome configurations with highest probability results for each node, which were organized decreasingly according to their likelihood value. The probability scores for these biome combinations were cumulative until a value of 0.5 was reached. The relative likelihood scores of each biome within these combinations were summed and all biomes with a cumulative likelihood of more 0.25 were retained for each node (Tables S3, S4). For example, if for a node the most probable biome combinations are I-II (presence in evergreen tropical rainforest and tropical deciduous woodland) with a likelihood value of 0.4, and II-II/III (presence in tropical deciduous woodland and savanna), with 0.12, this would imply that the values of relative probability for each biome are defined as follows: I=0.4, II=0.52 and II/III=0.12. We would then consider that only biomes I and II are robustly reconstructed for that particular node.

With the results for biome occupation in each node of the tree (Fig.1, Fig.4), we described the occupation trends of the different biomes through time. In order to assess the phylogenetic biome conservatism tendencies for both groups, we counted the transitions between biomes from each node to its descendant nodes. We then evaluated the relationship between historical biome dynamics and the development of new climatic niche by adaptation in the evolution of the lineages.

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In order to explore the biome colonization dynamics in each biome, we established the colonization events that explain the nodes states along the branches of the tree. However, the transition events have a temporal uncertainty, which is proportional to the branch length. Likewise, the phylogenies present a trend to increase the amount of branches along time producing an important bias towards present. To solve these issues, we analysed the biome colonization through time using a *sliding window* method. This approach was employed to calculate the mean and the confidence interval of colonization rates in each biome considering 1 million years time intervals and smoothed with a 5 million years sliding window that includes a correction factor taking into account the number of branches during each time bin (Vieites et al. 2007; Meredith et al. 2011).

4.4. RESULTS

4.4.1. *Ancestral Biome occupancy reconstruction in Galliformes*

Our analysis reconstructed ancestral biome occupancy for 220 nodes (98.21%); the remaining 4 nodes presented low statistical support for any of the ten biomes (Table S3). The common ancestor of the Galliformes was associated during the Late Eocene with tropical rainforest, tropical deciduous forest, savanna and temperate evergreen forest biomes (Fig.1). According to the results for biome occupancy patterns in Galliformes, this lineage presented three main moments of diversification: First, since early to middle Miocene, Phasianidae family presented an important radiation associated mainly with tropical deciduous forest. Likewise, during this period was recorded an important colonization of broadleaf deciduous forest, which allowed then the subsequent colonization of temperate and cold biomes; secondly, along the Late Miocene the fowl tropical families Megapodiidae, Numididae, Cracidae and Odontophoridae experimented a prominent process of diversification in Australasia, Afrotropics and Neotropics respectively. Despite their isolation, showed a close relationship with tropical deciduous forest, savannas and temperate evergreen forest. Conversely, some phasianid lineages (Tetraonini) radiated colonizing new cold biomes such as taiga. Finally, along the Plio-Pleistocene, Galliformes lineages reached their higher radiation and especially phasianidae species entered diverse emerging and extending biomes during glaciation periods such as sclerophyllous woodland-shrubland, deserts and steppes (Zimov et al. 1995; Douglas et al. 2006; Senut et al.

2009). Other biomes as evergreen rainforest and temperate evergreen forest also increased their number of invasions possibly because of the fragmentation and expansion that underwent during the glacial periods (Jaramillo et al. 2006; Werneck et al. 2011; Jaramillo 2012; Raes et al. 2014; Woodruff 2010).

Considering families (Fig.1), Megapodidae showed an ancestral biome occupation within the tropical deciduous forest and savanna, while Cracidae presented an ancestral occupation associated with tropical deciduous forest and temperate evergreen forest. It is interesting the differentiation pattern in two main clades of Cracidae, which reflected trends in the climate niche evolution towards temperate evergreen forest in the case of the subfamily Penelopinae and tropical deciduous forest in the clade that contains the rest of subfamilies. Ancestral biome for Numididae reflected an early occupation of savannas. The reconstruction for Odontophoridae showed an uncertain state for the ancestral biome occupation and two unresolved nodes inside the family. This result was probably due to the incomplete knowledge of phylogenetic relationships within this family, especially in *Odonthophorus*, which impeded the inclusion of climatic information for all species. However, our results showed a clearly differentiation in the principal lineages with species radiated towards two climate niches associated with tropical deciduous forest and temperate evergreen forest biomes.

Finally for the most specious Phasianidae, we found an ancestral biome occupation of tropical deciduous woodland and early diversification during the middle Miocene associated with this biome (Fig.1). Tropical deciduous woodland was ancestral biome of subfamily Rollulinae from Southeast Asia. Meanwhile, several tribes of Phasianinae (Coturnicini, Polyplectronini, Pavonini and Gallini) with an important geographical distribution in Africa and Asian Southeast also showed a diversification pattern within tropical deciduous forest, which is conserved along many clades of Phasianinae. Likewise, during the middle Miocene one lineage of phasianids would reach to colonize the temperate broadleaf deciduous forest. Within this lineage, the tribe Tetraonini ancestors entered in the boreal coniferous forest during the late Miocene. This group showed important biome conservatism associated with the taiga biome during its radiation. Other lineages such as Lophophorini independently occupied the boreal coniferous forest at the same moment that Tetraonini. On the other hand, Phasianini tends to preserve the

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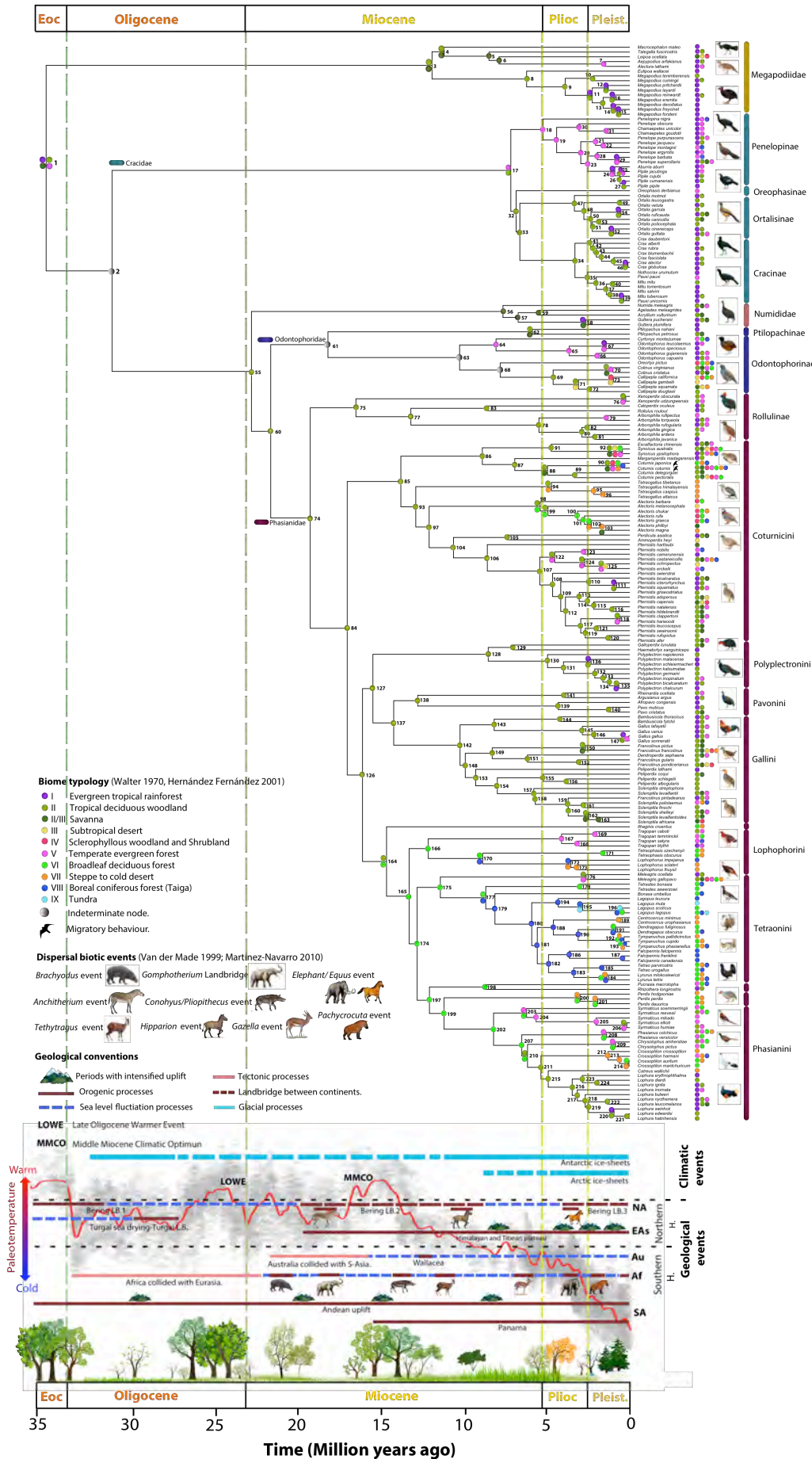
ancestral biome occupation in the broadleaf deciduous forest with subsequent colonizations of temperate evergreen forest and tropical deciduous forest (Fig.1).

According with the general tendencies, the results suggest different phases of biome colonization (Fig.2); during the early Oligocene the tropical deciduous woodland and the temperate evergreen forest presented an outstanding growing. In the Oligocene-Miocene boundary, the savanna registered an increase of new species. Meanwhile, the rates of colonization decrease in tropical deciduous woodland and the temperate evergreen forest during the same period. Later, along the middle and late Miocene we evidenced a marked growth in the colonization rates for the majority of biomes. Biomes such as evergreen tropical rainforest experimented a prominent increase of colonizations until the Pleistocene. Furthermore, emerging biomes such as deserts, sclerophyllous woodland-shrubland, steppe and taiga, represented new ecological opportunities for novel lineages. The new but limited niches probably allowed early increase of colonization events with subsequent stabilization as was observed for many seasonally biomes in boreal and subtropical latitudes.

Transitions among biomes are shown in Fig.3. We found important support for phylogenetic biome conservatism in the evolution of Galliformes. Biome occupancy was conserved along the phylogeny in 475 of 767 transition events (61.92%) while the biome shifts were represented by 292 possible invasion events (38.07%) (Table 2, Fig.3). The frequency of transitions between biomes reflects a higher signal of biome conservatism (%BC). All the biomes, except the savanna and sclerophyllous woodland-shrubland, presented values for biome conservatism higher than 50% with more elevated values (>75%) associated with biomes occupying the climate extreme gradient: evergreen tropical rainforest (82.93%), steppe (83.78%) and tundra (100%)(Table 2). The directional patterns in transition among biomes showed a predominant bias, with the tropical deciduous woodland as net species source for other biomes in tropical and subtropical latitudes.

Figure 1. Ancestral biome reconstruction for Galliformes. The colors represent the 10 different biomes implemented in the model (Walter 1970, Hernández Fernández 2001). For each node, the colored circle represents the inferred biome (s) on all the nodes. The colors in the tips correspond with the recent biome distribution of species. Along the time scale, geological and climatic histories are shown as well as intercontinental biotic interchanges. LB: Landbridge; NA: North America; EAs: Eurasia; Au: Australia; Af: Africa; SA: South America.

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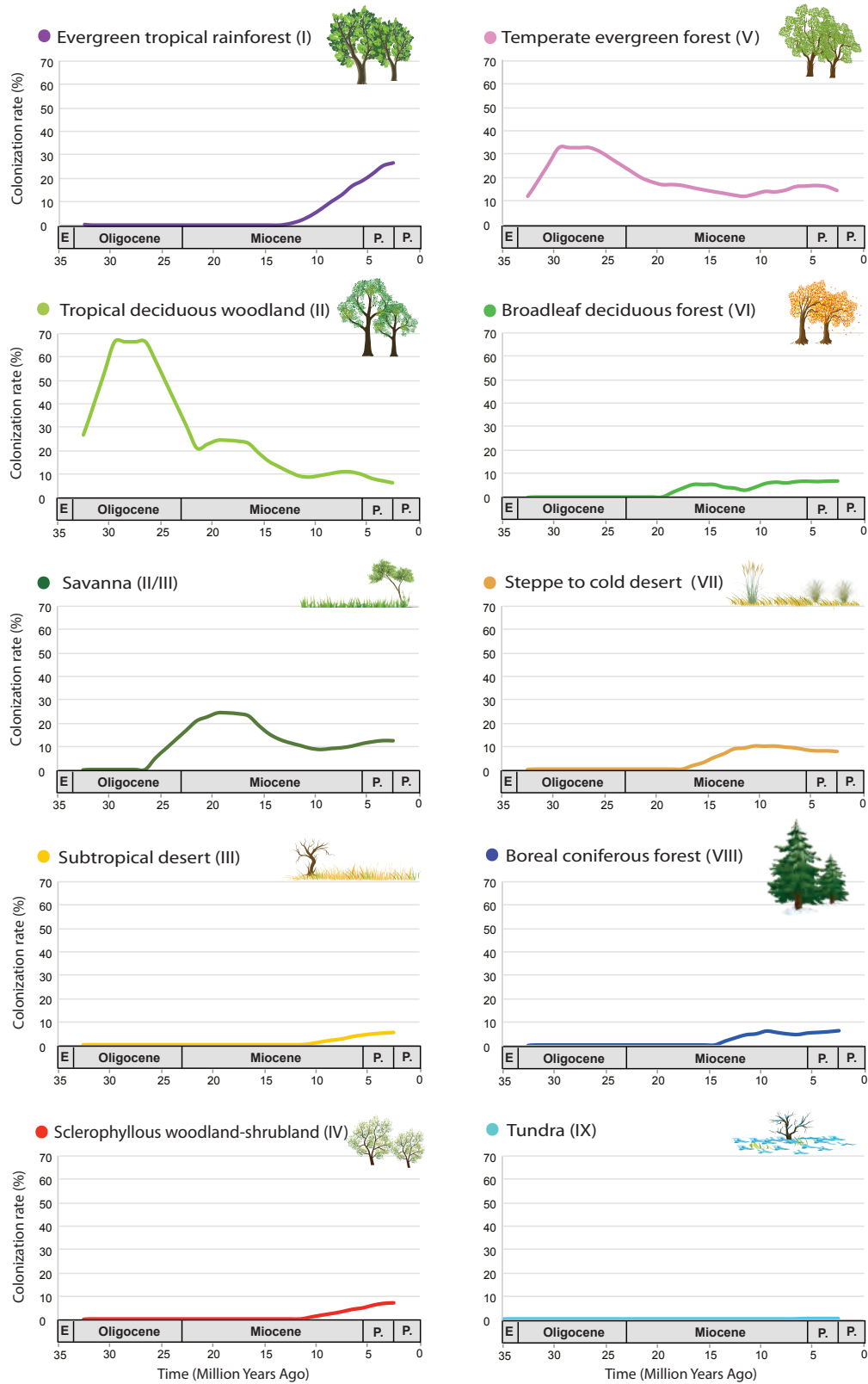


Figure 2. Colonization dynamics of Galliformes. For each biome is represented the rate of colonization by new lineages along the geologic time.

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Table 2. Biome transitions in Galliformes

BIOME	Destination											
Source	I	II	II/III	III	IV	V	VI	VII	VIII	IX	Total col.	% BC
I	34	4	1			2					7	82.9
II	55	225	34	10	7	29	7	7			149	60.2
II/III	7	5	23	2	4	3	2	4			27	46.0
III				5	1		1	2			4	55.6
IV					3		1	3	1		5	37.5
V	20	13	3		1	67	5		10		52	56.3
VI		3		1	4	4	54	10	6		28	65.9
VII					1		1	31	4		6	83.8
VIII							7	6	30	1	14	68.2
IX										3	0	100.0

Number of biome transitions for each biome considering the source (rows) and destination (columns). Bold numbers along the diagonal show transitions with no change of biome (**475**). Total col. on the right indicates the transitions that imply colonization (**292**). % BC, represents the proportion of biome conservatism for each biome according to colonization tendencies. The total number of transitions was 767.

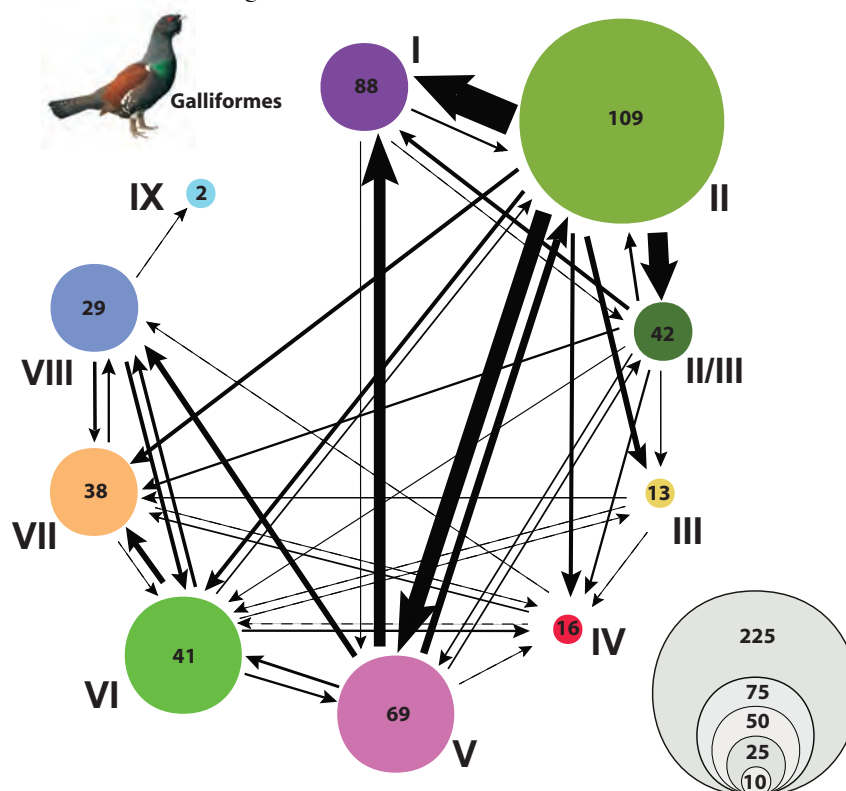


Figure 3. Biome transitions in Galliformes. Number of recent species is indicated inside the circle. Arrow thickness is proportional to the number of colonizations, the dashed lines indicate only one colonization event. The number of transitions that not implied colonization is indicates as different ranges in the circles area classified in five categories (see diagram). For more details about absolute scores see Table 2.

4.4.2. Ancestral Biome occupancy reconstruction in Falconiformes

We reconstructed the ancestral biome occupancy for 60 of 65 (92.31%) nodes in the phylogenetic tree of Falconiformes (Table S4, Fig.4). Our findings suggest that the early Oligocene ancestor of falcons probably occupied environments associated with tropical biomes such as evergreen tropical rainforest, tropical deciduous woodland and savannah (Fig.4). During lower and middle Miocene the Falconiformes basal lineage (Herpetotherinae) extended towards temperate evergreen forest, but conserved the association with forested tropical biomes and savanna. Finally, along the Pliocene this lineage diversified into the tropical rainforest and deciduous forest. Poliborini and Falconini diverged during the middle Miocene conserving the ancestral biome occupancy. Our results indicate an initial colonization from tropical biomes to temperate environments by Poliborini ancestors during the late Miocene with a subsequent specialization towards tropical seasonality and drier environments as tropical deciduous forest and savanna along the late Miocene and Pliocene; Poliborini tended to develop a generalist spectrum with broad biome occupancy in the Pleistocene. The divergence within Falconini appears to be related to the *Falco* colonization process of savannas and tropical deciduous woodlands during the middle Miocene, while *Microhierax* and *Polihierax* ancestors specialized in savanna environments. Subsequently *Falco* expands from tropical forest environments and savannas towards temperate biomes since the late Miocene (Fig.4). During the late Miocene and Pliocene there was a high speciation in falconid lineages, more highlighted in *Falco*, which was mainly associated with tropical deciduous forest and savannas. During the Pliocene falcons colonized biomes such as broadleaf deciduous forest. Likewise, along the Plio-Pleistocene also were colonized novel and emerging biomes such as desert, sclerophyllous woodland-shrubland and steppe.

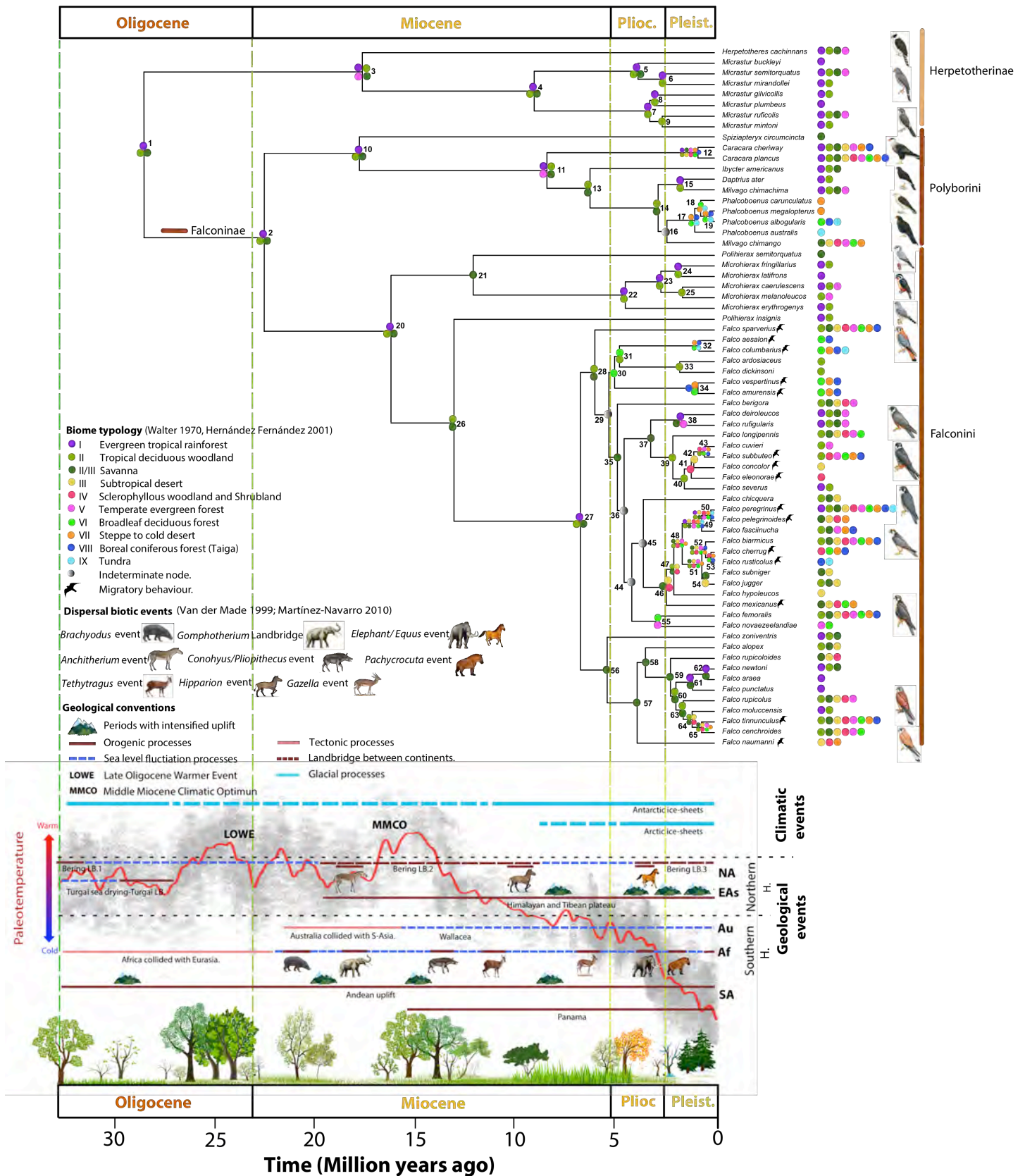
In general terms, the patterns of biome colonization along time in Falconiformes (Fig.5) showed low trends in the colonization of new biomes during their early evolution in the Oligocene and early Miocene. In this period only was colonized the temperate evergreen forest. It would be later, during the middle Miocene when the falconid lineages began to colonize tropical biomes such as evergreen tropical rainforest and tropical deciduous woodland. During late Miocene, began an outstanding process of colonization in all biomes.

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The results for biome transitions pattern in Falconiformes (Table 3, Fig.6) showed similar values for biome conservatism respect to Galliformes. The biome was conserved in 273 of 436 (62.61%) possible biome transitions during cladogenesis events. Meanwhile 37.39% corresponds to 163 new biome colonization events (Table 3, Fig.6). The obtained frequencies of transitions between biomes showed a significant proportion of biome conservatism with respect to the invasion of new environments. In the case of Falconiformes, all the biomes presented higher values of biome conservatism (%BC), which were higher than 50%. The highest scores were registered for biomes such as evergreen tropical rainforest (82.5%), steppes (77.8%), taiga (93.8%) and tundra (87.5%). These results also showed a prominent directional bias in the transitions among biomes, the outcomes suggest an important role of tropical deciduous woodlands and savannas being net sources of species and the evergreen rainforest and temperate evergreen forest as sink. It is interesting that savanna constitutes an important destination from lineages coming from tropical deciduous woodlands (Table 3, Fig.6).

Figure 4. Ancestral biome reconstruction for Falconiformes. The colors represent the 10 different biomes implemented in the model (Walter 1970, Hernández Fernández 2001). For each node, the colored circle represents the inferred biome (s) on all the nodes. The colors in the tips correspond with the recent biome distribution of species. Along the time scale, geological and climatic histories are shown as well as intercontinental biotic interchanges. LB: Landbridge; NA: North America; EAs: Eurasia; Au: Australia; Af: Africa; SA: South America).

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4. Phylogeny and biome occupancy

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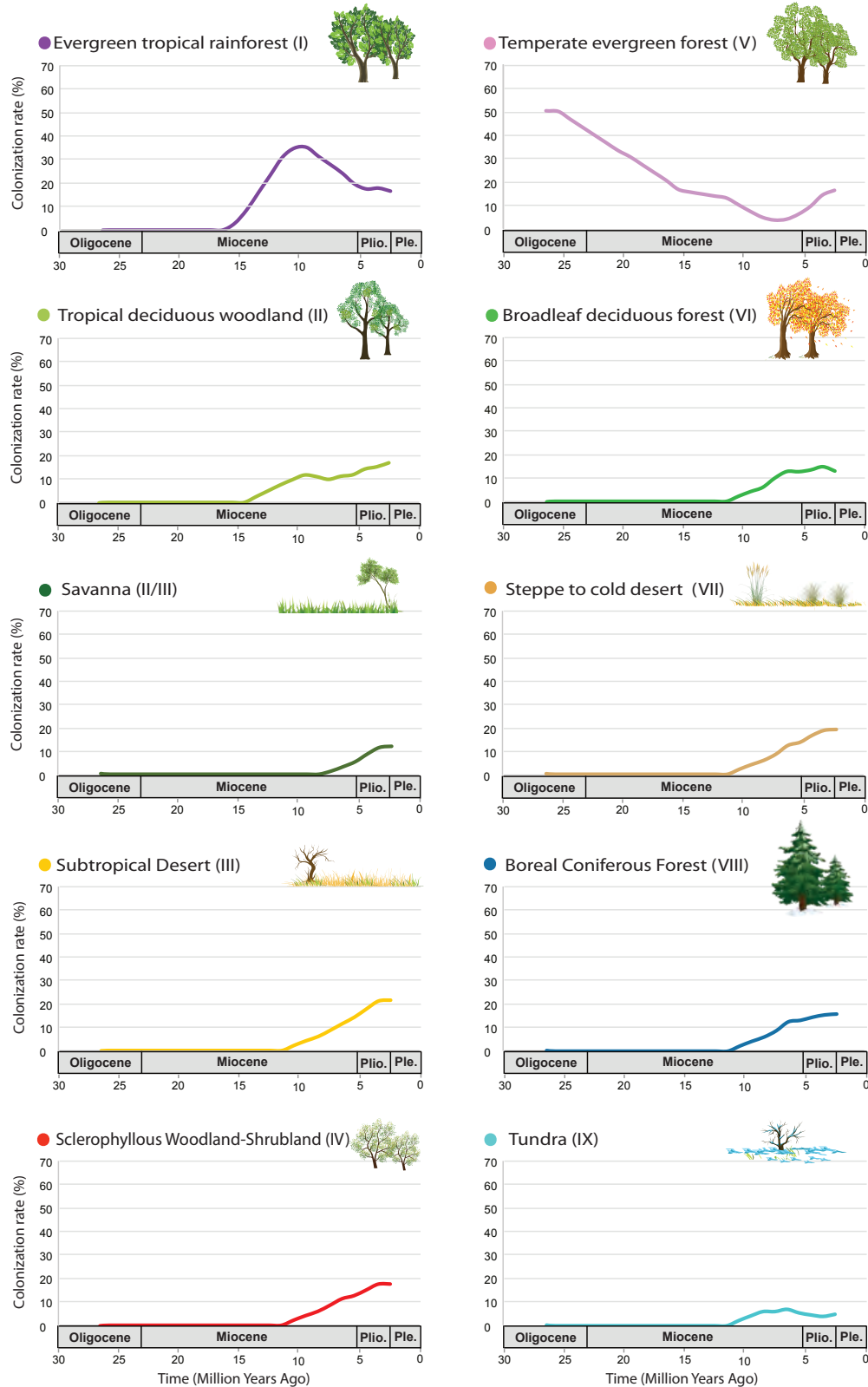


Figure 5. Colonization dynamics of Falconiformes. For each biome is represented the rate of colonization by new lineages along the geologic time.

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Table 2. Biome transitions in Falconiformes

BIOME	Destination										Total col.	%BC
Source	I	II	II/III	III	IV	V	VI	VII	VIII	IX		
I	33	3	2			2					7	82.5
II	11	61	4	4	5	12	5	1			42	59.2
II/III	8	10	57	8	7	7	4	6			50	53.3
III		3		20	1		4	4			12	62.5
IV		1		1	18	2	3	3			10	64.3
V	1	3	1		1	18	1		6		13	58.1
VI		2	1	1	2	1	23	4	8	2	21	52.3
VII								21	5	1	6	77.8
VIII									15	1	1	93.8
IX									1	7	1	87.5

Number of biome transitions for each biome considering the source (rows) and destination (columns). Bold numbers along the diagonal show transitions with no change of biome (273). Total col. on the right indicates the transitions that imply colonization (163). % BC, represents the proportion of biome conservatism for each biome according to colonization tendencies. The total number of transitions was 436.

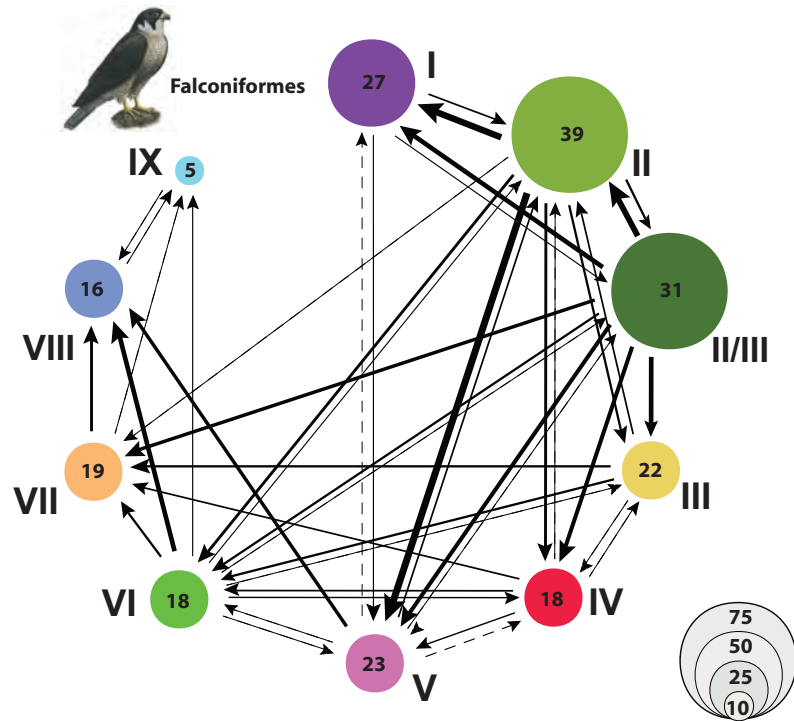


Figure 6. Biome transitions in Falconiformes. Number of recent species is indicated inside the circle. Arrow thickness is proportional to the number of colonizations, the dashed lines indicate only one colonization event. The number of transitions that not implied colonization is indicates as different ranges in the circles area classified in four categories (see diagram). For more details about absolute scores see Table 3.

4.5. DISCUSSION

4.5.1. *Galliformes history and biomic occupancy patterns*

Our results proposed generalist biome occupancy in basal crown Galliformes with ancestral presence in evergreen tropical rainforest, tropical deciduous forest, savanna and temperate evergreen forest (Fig.1). This broad ancestral occupancy is consistent with the early evolution of Galliformes. The first unambiguous presence of Galliformes in the fossil record is Paleocene (Mayr 2009; Hwang et al. 2010). Paleocene and Eocene species represent *stemgroup* families, which reached great diversity in the Northern Hemisphere (Mayr 2009). The earliest stem-family Gallinuloididae, would have spread by moist forest ecosystems in Europe and North America during the early and middle Eocene (Mayr and Weidig 2004), periods with warm climate (Zachos et al. 2001; Fine and Ree 2006; Zachos et al. 2008). Anatomical traits relative to the furcula and *sternal carina* in Gallinuloididae indicate the possible presence of an undeveloped crop respect to derivate lineages. In addition, none of known fossil specimens preserved gastroliths for mechanical digestion of hard plant matter such as seeds (Mayr and Weidig 2004; Mayr 2009). These evidences suggest that dietary requirements in early galliforms consisted of fruit and other soft vegetable material, which is consistent with occupation of the warm and wet tropical forested biomes predominant during the Eocene. Likewise, our findings agree with the broad biome distribution and dietary innovations inferred for the ancestral stem lineage Quercymegapodidae, which is phylogenetically closest to the crown Galliformes. This lineage inhabited the late Eocene forest environments in Europe and South America (Mourer-Chauviré 1992; Mayr 2009) and showed the first evidence of gastroliths in landfowls (Mayr 2009). This adaptation implied a high digestive capacity to process different sources of plant matter suggesting a great versatility to exploit novel feeding resources provided by the colonization of emerging semiarid and temperate biomes during the late Eocene and early Oligocene (Retallack 1992; Jacobs 2004; Jaramillo et al. 2006; Lindow and Dyke 2006; Werneck et al. 2011; Jaramillo and Cárdenas 2013). Global temperature decrease and the aridification towards the Eocene-Oligocene boundary (Zachos et al. 2001) are possibly related to the broad biome occupancy of crown-Galliformes ancestors. This would be a response to the fragmentation of evergreen tropical rainforests with expansion of tropical deciduous woodlands and savannas vegetation derived from a

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strong seasonality in precipitation (Woodward et al. 2004). Our results showed a subsequent process of specialisation in tropical deciduous woodland and the withdrawal of the evergreen tropical rainforest and temperate evergreen forest in several Oligocene lineages (Fig.1).

Along the Oligocene and the Miocene, the tropical deciduous woodland biome would have played an important role in the diversification of the main clades of Galliformes. During this period the evolution of ancestral occupation for main clades conserved the presence in this biome. The digestive versatility in relation to novel plant sources during dry periods probably was a key factor to explain the observed trends in specialization and biome conservatism in the tropical deciduous woodlands. Likewise, this trait would have allowed the colonization of other emerging seasonal biomes with plants adapted to arid and dry conditions such as savanna or steppe (Fig.1). In general, the tropical deciduous woodland probably was conserved because their niches evolved in close relationship with seasonal aridity in tropical and subtropical latitudes (Pennington et al. 2004b). According to paleoclimatic evidence of plant and pollen fossils, dry forested and semi-open grassland ecosystems presented a continuous expansion along the Miocene to present times (Burnham 1995; Wang et al. 2014; Lavin et al. 2005).

Our results showed that Megapodidae extended during the middle and late Miocene across the tropical deciduous woodland biome arising in Australia and adjacent islands (Pennington et al. 2004a; Martin 2006; Byrne et al. 2008) (Fig.1). During the Pliocene some lineages (i.e. *Megapodius*) colonized the evergreen tropical rainforest environments in diverse periods (Fig.1). Due to the vicariance processes in the last 3 million years associated to geographic isolation of rainforest fragments in relation to cooling periods during glacial periods and sea level elevations by interglacial periods many species diversified in this biome (Williams and Pearson 1997; Voris 2000; Meijaard 2003; Filardi and Moyle 2005; Woodruff 2010; Harris et al. 2014).

Cracidae subfamilies diverged during the late Miocene towards two climatic niches (Figures 1). According to fossil evidence, ancestral cracids such as *Ortalis* inhabited the Miocene of North America (Wetmore 1930), which presented dry open and semi-open environments such as tropical deciduous woodland (Wang et al. 1994; Pound et al. 2012). Our results suggest a divergence process in biome

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occupancy during the late Miocene, which would be supported by the closure of the Panamanian land bridge during the Miocene (Hoorn and Flantua 2015; Montes et al. 2015) allowing the entering in South American environments (Weir et al. 2009). The initial colonization of temperate evergreen forest probably was related to the intense period of mountain building in Panama landbridge, previous to the dispersal into South America (Hoorn and Flantua 2015). During the orogeny, when a critical elevation is reached (1500 - 2000 m), the temperature drop probably altered the precipitations and increased the humidity, which established the new montane forest (temperate evergreen forest biome analogous) of the highlands of Central and South America (Holdridge 1967; Renjifo et al. 1997; Hoorn et al. 2010). The emerging of montane biome would allow the specialization of Penelopinae in new niches while another clade including the rest of subfamilies specialized in tropical deciduous woodland. Finally, our findings suggest several independent colonization events for the evergreen tropical rainforest during the Pleistocene. During the dry periods related with the glaciations, the isolation of rainforest fragments near areas in the periphery of Amazonia were separated by dry forest and savannas, along dry climatic periods (Haffer 2008). This scenario would allow the vicariance in the refugia according with the specialization processes of many taxa within this biome (Bennett et al. 2012; Jaramillo 2012). Likewise, the historical climatic dynamics of tropical evergreen rainforest in close association with deciduous woodland and temperate evergreen forest in mountains regions of tropical latitudes, allowed new colonization events between these biomes (Pennington et al. 2000; Hooghiemstra and Van der Hammen 2004; Haffer 2008). This is confirmed by our results as well as by other studies focussing on other rainforest taxa such as Cebidae monkeys (Alfaro et al. 2015), trumpeters (Ribas et al. 2011) and parrots (Ribas et al. 2009; Quintero et al. 2013).

Numididae apparently evolved under the influence of the African aridification of the late Neogene (Bobe 2006; Hernandez Fernandez et al. 2007; Senut et al. 2009). The observed specialization and biome conservatism of savannas during most of the evolutionary history of Numididae (Figures 1) is in concordance with the increase of open and arid habitats dominated by C4 grasslands in Africa since the late Miocene (Pickford 1992; Jacobs 2004; Beerling and Osborne 2006; Edwards et al. 2010). The seasonal climatic similarity between tropical deciduous woodland and savanna, probably allowed the adaptation of guinea fowl lineages to these conditions

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(Davies 1982; Dean et al. 2009). Along Plio-Pleistocene glaciations, there was an intense aridification of Africa (de Menocal 2004; Sepulchre et al. 2006; Senut et al. 2009) and an important reduction of rainforest areas (Plana 2004) with a consequent increase of savannas (Jacobs 2004; Bouchenak-Khelladi and Hodkinson 2011). According to this, during the savannas driest periods, the arid conditions might promote diverse adaptations and nomadic habits (Tieleman et al. 2003), which facilitated dispersal events towards zones with water availability in ecotone areas of savanna with tropical deciduous woodlands and evergreen tropical rainforests (Lloyd 1999; Dean et al. 2009). These habits may have favoured the colonization of tropical evergreen rainforest in equatorial Africa and tropical deciduous woodlands biomes conserving the ancestral savanna occupation.

The family Odontophoridae diverged in two basal lineages. First, the African Ptilopachinae (Cohen et al. 2012) showed a biome occupancy associated with the savanna and tropical deciduous woodland during the late Miocene, in a aridification-driven pattern that resembles that of Numididae (Jacobs 2004; Senut et al. 2009). The American Odontophorinae presented two main tendencies of biome occupancy in Nearctic and Neotropics. North American ancestors of lineages as *Colinus* and *Callipepla* inhabited tropical deciduous forest and were able to colonized during the Plio-Pleistocene other dry and relatively open environments such as savannas, deserts and sclerophyllous woodland-shrublands. This process would be associated to geological and climatic events in relation to the Sierra Madre plateau uplift between the late Miocene and Pliocene, sea transgressions in the California Peninsula during different moments since the Miocene, and Pleistocene glacial-interglacial alternance (Zink and Blackwell 1998; Riddle and Hafner 2006). Meanwhile, for Neotropics, our results suggest process of colonization of temperate evergreen forest between late Miocene and early Pliocene for the clade that includes *Odontophorus* species (Fig.1). This is consistent with the origin of montane environments in Central and South America during the uplift of the Panamanian landbridge and the subsequent phases of elevation in the northern Andes (Hoorn et al. 2010; Montes et al. 2012; Montes et al. 2015), which propitiated vicariance similarly to what has been found in other bird groups (Fjeldsa^o 1992; Quintero et al. 2013; Sweet and Johnson 2014). In general, these results show broad consistency with the patterns previously explained for Penelopinae, which suggests a common historical context for parallel evolution of Neotropical montane groups in relation to the biomes dynamics.

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Whereas Numididae specialized in savanna environments, Phasianidae ancestors conserved the ancestral occupation associated with tropical deciduous woodland environments reaching a prominent diversification during the middle and late Miocene within a context of high biome conservatism (Fig.1). The fossil record suggest a broad distribution of Phasianidae in Eurasia around the late Oligocene to middle Miocene (Li et al. 1983; Rich et al. 1986; Sánchez Marco 1999; Mayr 2009; Zelenkov 2009), These basal phasianids were associated with dry and seasonal forest environments, which emerged in many regions in relation to the increasing of dryer and cooler conditions that fragmented originally moist forest areas (Zachos et al. 2001; Guo et al. 2008; Bozukov et al. 2009; Ivanov et al. 2011).

Along the diversification of Phasianidae (Fig.1) our results suggest influence of biotic interchange events between Europe, Asia, and Africa in the occupancy of different biomes. During the early Miocene, Africa-Arabia collided with Eurasia. This event altered the atmospheric circulation and at the same time the rifting and local uplift blocked the flow of humidity across Africa (Pickford 1992; Bobe 2006; Sepulchre et al. 2006; Senut et al. 2009). The widespread evergreen tropical rainforest was fragmented and replaced by tropical deciduous woodland with many seasonal forest environments (Jacobs 2004; Plana 2004; Bobe 2006). Our findings suggest that *Xenoperdix* clade diverged from *Arborophila* clade invading Africa during the early Miocene probably through the *Gomphotherium* land bridge around 18 Ma (van der Made 1999; Koufos et al. 2005). The interchange between Eurasia and Africa for Galliformes was possible during many periods along the Miocene, while the seasonal conditions of tropical deciduous woodland and savanna existed in Arabia, before the Plio-Pleistocene desertification and isolation by the Red Sea (Dinesen et al. 1994; Pound et al. 2012). Precisely, clades such as *Pternistis* (Coturnicini) and *Francolinus* and allies (Gallini) represent a parallel colonization of African tropical deciduous woodlands during Late Miocene in concordance with the *Hipparion* event (van der Made 1999). These lineages preserved their ancestral biome and reached a high ecological diversification, colonizing possible emerging dry woodland in Africa caused by rainforest contraction (Crowe et al. 1992; Pickford 1992; Jacobs 2004; Pound et al. 2012).

Considering Coturnicini, clades such as *Coturnix* and *Synoicus* with origin in tropical deciduous woodland showed a generalist biome occupation possibly related

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with the development of migration behaviour and physiological versatility, which allowed them to achieve a high dispersal capacity and colonized a broad variety of biomes (Rolland et al. 2014; Pelegrin et al. 2015) reaching a wide geographical distribution in Eurasia and even Australia during the Pliocene and Pleistocene. The Coturnicini temperate clades showed two main colonization events from their ancestral biome: the steppes colonization by *Tetraogallus* and the occupation of broadleaf deciduous forests by *Alectoris*. In the case of *Tetraogallus*, the evolution of snowcock in central Asia is consistent with cooling process during the late Miocene and the orogeny processes triggered by the Tibetan Plateau and Caucasus uplift (van Dam 2006; An et al. 2015). Progressive vegetation changes and arising of cold and open environments in central Asia drove the colonization and subsequent specialization in emerging steppes; the glacial interglacial alternance caused the fragmentation of snowcock steppe habitats, resulting in the isolation of populations in mountainous systems and subsequent speciation events during the Pleistocene (Yang et al. 2009; Qu et al. 2010; An et al. 2015). *Alectoris* ancestors during the late Miocene colonized the broadleaf deciduous forest from tropical deciduous woodland, which expanded along central and east Europe regions during middle and late Miocene (Pound et al. 2012). Subsequently, vicariance between Southern Europe and Northern Africa was possible under the influence of the Messinian event and the Zanclean flood (Garcia-Castellanos et al. 2009). The Eurasian populations adapted initially to tropical deciduous woodlands, colonized the broadleaf deciduous forests, which were present during the early Pliocene in continental Europe and the Mediterranean basin (Hernandez Fernandez et al. 2007). The continuing global cooling process caused the specialization in broadleaf deciduous forests. Our results suggest diversification by colonization of sclerophyllous shrubland-woodland and steppe environments from broadleaf deciduous forest during the Pleistocene, which is consistent with the origin of sclerophyllous environments (Hernandez Fernandez et al. 2007; Buerki et al. 2012) and the refugia model for Mediterranean fauna (Hewitt 2003; Sánchez Marco 2004; Ferrero et al. 2011; Abellán and Svenning 2014).

The Eurasian most specious phasianid lineages present two main tendencies in their biome occupancy patterns. The results suggest a divergence process c.a 15 Ma associated with the colonization of broadleaf forest by the clade Lophophorini-Tetraonini-Phasianini while the lineage Polyplectronini-Pavonini-Gallini conserved the ancestral occupation in the tropical deciduous woodland. This suggests an initial

dispersal scenario towards temperate latitudes following a reinforced latitudinal temperature gradient of the Mid-Miocene Climatic Optimum (Zachos et al. 2001). Around this time, the biomes configuration was constituted by boreal coniferous forest at the high northern latitudes, extensive warm-temperate mixed forest in the middle and subtropical latitudes and finally, tropical forest biomes in tropical and equatorial latitudes (Pound et al. 2012). The Himalayan and Tibetan plateau orogeny constituted a geographical barrier that possibly had a significant influence on the separation and later diversification of both lineages. The Tibet system experimented during the early Miocene (20 Ma) a gradual elevation increase and would reached its present configuration around 8 Ma (Miao et al. 2012; Lei et al. 2014). However there is a broad debate that propose a more recently uplift process (Lei et al. 2014). The recent geological history of Himalayas and Tibetan Plateau includes different events (Spicer et al. 2003; Yang et al. 2009; Lei et al. 2014) that caused important climatic and ecological changes (Guo et al. 2008; Liu et al. 2009; Yao et al. 2011; Miao et al. 2012; Pound et al. 2012), including an intensification of cooling and aridification in central Asia and the increase of the monsoon regime in the southern and eastern Asia (Shi et al. 1999; Zheng et al. 2004; Liu et al. 2009). Every uplift event produced a fragmentation of biomes by modification of the local precipitation patterns, creating novel scenarios for vicariance of the tropical lineages Polyplectronini, Pavonini and Gallini in the tropical deciduous woodlands of India and Indochina (Zhisheng et al. 2001; Zheng et al. 2004; Yao et al. 2011; Miao et al. 2012).

The ancestral biome occupancy in broadleaf deciduous forest of Lophophorini and its geographical distribution suggest an initial process of colonization of arising biomes with the Tibetan system formation. During the late Miocene and early Pliocene there was a colonization of emerging mountain biomes such as boreal coniferous forests and steppes during the progressive uplift, the global cooling and aridification (Wen and Liu 2010). During the middle Miocene Tetraonini branched off from Phasianini conserving the occupation of broadleaf deciduous forest biome. This biome conservatism and the geographic distribution of the implied clades suggest a second event of isolation under the influence of the Tibetan Plateau uplift. According to this, the Tetraonini ancestors would colonize the northern areas of broadleaf deciduous forest at high latitudes. The northwards expansion of Tetraonini can explain the divergence process that caused the separation of turkeys lineage c.a 11

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Ma, possibly caused by the colonization of North America through the ‘*Hipparion* landbridge’ (van der Made 1999). Around the late Miocene, Tetraonini as well as Lophophorini colonized the taiga biome favoured by global cooling and the extension of this biome towards southern latitudes, reducing the predominance of temperate environments (Pound et al. 2011; Miao et al. 2012). The grouses diversified within the boreal coniferous forest biome possibly through the development of new physiological adaptations to the cold conditions of this environment (Andreev 1988). Likewise, the biome occupation associated with cold environments would have allowed their spread throughout Europe and the colonization of North America via the Bering Landbridge in diverse episodes during the so called ‘Elephant-*Equus* event’ (Martínez-Navarro 2010) and Pleistocene glaciations (Ogasawara 1998; Marincovich and Gladenkov 2001). The adaptations to colder conditions would have acted like as constraint in the adaptation to other climates regime, allowing only to colonize emerging cold biomes such as steppes and the arctic tundra during the Plio-Pleistocene (Weir and Schluter 2004).

On the other hand, the results for Phasianini showed the conservatism of broadleaf deciduous forest occupancy during its early cladogenesis. These findings suggest the colonization and subsequent vicariance in temperate biomes east of the Tibetan plateau, which might have relation with the late Miocene and Pliocene tectonic processes in Tianshui-Huicheng region that caused the formation of barriers and valley systems (Miao et al. 2012). This scenario promoted the emergency of diverse vicariance events and new biomes in highlands and lowlands of subtropical latitudes from China as well as influenced the relocation of atmospheric water from monsoon in the Eastern Asia (Shi et al. 1999; Wang et al. 2011; Miao et al. 2012) changing the regional biomes configuration. This enabled speciation in temperate evergreen forest and broadleaf deciduous forest at lowland lineages such as *Syrnaticus* or in mountain environments for *Perdix* and *Crossoptilon* lineages (Lei et al. 2014). During the late Miocene, the *Lophura* lineage spread towards the tropical deciduous woodland, which expanded across important areas in the South East of Asia due to the monsoon climate regime (Zhisheng et al. 2001; Zheng et al. 2004). These novel conditions promoted the emergency of new niches and the subsequent colonization of tropical deciduous woodland in tropical latitudes by lineages coming from broadleaf deciduous forest in subtropical ones. Our results for Phasianini are broadly consistent with the recent geographical distribution patterns and the high level of endemism

reported for Chinese mountain areas and forest environments in the Asian South East (Lu et al. 1997; Randi et al. 2001; Huang et al. 2009; Lei et al. 2014).

4.5.2. *Falconiformes history and biomic occupancy patterns*

The reconstruction of ancestral biome occupancy in Falconiformes (Fig.4) during the Oligocene reveals an origin associated with tropical biomes: evergreen tropical rainforest, tropical deciduous woodland and savanna. These findings are consistent with Falconiformes originating in the Neotropics. This origin is supported by the presence and diversification of endemic basal lineages (Herpetotherinae and Polyborini) (Fuchs et al. 2011; Fuchs et al. 2012). Also, the oldest record for crown clade Falconidae (*Pedohierax* and *Thegornis*) is Neotropical (Tambussi et al. 1995; Noriega et al. 2011; Tambussi and Degrange 2013). Finally, under a phylogenetic point of view, Falconiformes is part of the Australaves clade (Falconiformes, Cariamiformes, Psittaciformes and Passeriformes), which presumably evolved in South America-Antarctica-Australia-Zealand (Ericson 2012; Jarvis et al. 2014) (see also Chapter 3). At the Eocene-Oligocene boundary the opening of the Drake passage and the subsequent glaciation in Antarctica caused cooling and drying trend (Francis et al. 2008; Zachos et al. 2008), which triggered an important reduction of evergreen tropical rainforest in South America (Fine and Ree 2006; Jaramillo et al. 2006), and the expansion of drier environments such as tropical deciduous woodland and the initial emerging of savannas (Ortiz-Jaureguizar and Cladera 2006; Edwards et al. 2010).

During the Oligocene, the divergence between Herpetotherinae and Falconinae probably was influenced by diverse processes such as the establishment of an ecological gradient triggered by the Oligocene cooling trend, the beginning of Andean orogeny and the Oligocene-Miocene sea transgression (Lundberg et al. 1998; Ortiz-Jaureguizar and Cladera 2006; Tambussi and Degrange 2013). These processes would have promoted vicariance between both lineages. Herpetotherinae expanded towards northern and western areas following the Andean influence zone. Meanwhile, Falconinae ancestors would have spread eastwards to the Brazilian area.

The Herpetotherinae ancestors during the early Miocene colonized the temperate evergreen forest (Fig.4), this event was caused possibly by modification in the Andean arc (Uliana and Biddle 1988; Ortiz-Jaureguizar and Cladera 2006; Hoorn et al. 2010), which originated new montane environments with temperate conditions

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(Hoorn et al. 2010). During the middle Miocene *Herpetotheres* separated from *Micrastur*, probably *Herpetotheres* dietary habits such as exclusive snake hunter allow them occupy a specific ecological niche but achieve a broad geographical distribution (Ferguson-Lees and Christie 2001) in relation to the wide distribution and diversification that snakes species present in diverse habitats in the Neotropics during the Neogene (Cadle and Greene 1993; Daza et al. 2010; Pyron and Burbrink 2012). *Micrastur* showed a diversification pattern associated specially with tropical evergreen rainforest and tropical deciduous woodland. These results suggest that *Micrastur* species possibly were affected for diverse processes that fragmented these biomes since the middle Miocene and the Pliocene. During this time span, the consolidation of Pebas lake system (c.a 17-9 M.a) (Wesselingh and Salo 2006), the mountain building in the central and northern Andes (c.a 12 M.a) and the continuous uplift of Northern Andes that defined “Pan-Amazonia” region (c.a 10 M.a) (Lundberg et al. 1998; Campbell et al. 2006; Hoorn et al. 2010) were processes that would have promoted the initial divergence for the *Micrastur* lineages in two main clades (Fig.4). The broad geographic distribution reached by *M. semitorquatus* or *M. ruficollis* suggest that, despite their forested habitat preferences, these raptor-birds could develop a high dispersal capacity (Ferguson-Lees and Christie 2001), which might have allowed the expansion towards similar biomes through lowlands and Andean slopes in northern South America (Hooghiemstra and Van der Hammen 2004; Jaramillo and Cárdenas 2013).

The separation of *S. circumcincta* respect to the caracaras lineage (Fig.4) was triggered probably in relation to biome specialisation in the arising open and dry savannas in southern South America during the early Miocene (Pennington et al. 2004b; Ortiz-Jaureguizar and Cladera 2006). Conversely, the caracaras lineage conserved the ancestral generalist biome occupation, which allow them to spread towards biomes that were originated in different zones of Southern South America, especially in subtropical latitudes during Miocene cooling periods (Pound et al. 2012; Le Roux 2012). A body-size increase in the caracara lineage respect to *Spiziatpeyx* may have caused changes in the dietary spectrum related to their trend towards ecological generalization; the caracaras developed a generalist/scavenging-like behaviour (Ferguson-Lees and Christie 2001) that allowed them gradually to colonise many biomes during the Plio-Pleistocene. This pattern is consistent with the apparition and radiation of other biome generalist birds with scavenging habits in

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South America such as the New World vultures (Pelegrin 2009; Fuchs et al. 2012; Tambussi and Degrange 2013).

During the late Miocene the ancestors of the *Ibycter-Phalcoboenus* clade branched off from the *Caracara* lineage (Fig.4) possibly due to Miocene and Pliocene biome shifts that increased the dominance of tropical deciduous woodland and savannas in South America. The biome shifts and associated fragmentation probably generated process of vicariance in zones such as the Cerrado (tropical deciduous woodland) or the Caatinga (savanna) (Pennington et al. 2004b; Werneck 2011). The ecological relationship between these areas and the close evergreen tropical rainforest would lead to lineages such as *Ibycter*, *Daptrius* or *Milvago* to invade this environment during the rainforest contractions triggered by the Pleistocene glaciations. Meanwhile, *Phalcoboenus* lineage colonized during Pleistocene colder and more seasonal biomes. This lineage probably spread along the Andes mountain system conserving the presence in highland steppes and diverging by isolation of populations due to the glacial-interglacial cyclicity (Hooghiemstra 1989; Hooghiemstra et al. 1995; Ortiz-Jaureguizar and Cladera 2006).

Our findings presented a divergence between Polyborini and Falconini conserving the ancestral biome occupancy, which suggest a dispersal scenario out of South America colonizing the Old World during the late Oligocene. According to paleogeographical evidence, South America and Africa were closer during the late Oligocene (around 1800 km respect to 2900 km in modern times) (Scotese 2001). In addition, the basal position of *Polihierax* in Falconini clade and its anatomical and ecological features may suggest that ancestral Falconinae were small size species with pointed wings for fast undulating flight and dietary habits mainly associated with little animals such as insects or lizards (Del Hoyo et al. 1994; Kemp and Crowe 1994; Ferguson-Lees and Christie 2001). Considering this context, the hypothetical ancestral development of high flight capacity, the relatively proximity between South America and Africa, and the apparently low water dependence reported for the pygmy falcons (Anderson et al. 1999) probably were some important factors that eased the transoceanic dispersal (De Queiroz 2005; Gillespie et al. 2011). A similar scenario, but in other direction, has been proposed for bird taxa apparently exclusive from the Neotropics such as the hoatzin (Mayr and De Pietri 2014) as well as for mammals such as New World monkeys and rodents (Poux et al. 2006). The long-

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distance fly capacity legacy would have enabled *Microhierax* ancestors to expand into tropical deciduous woodland and evergreen tropical forest biomes in Indian subcontinent and southeast Asia by the “stepping stones” route formed in the Indian Ocean through Madagascar and Seychelles islands, which is proposed as an important bridge between Africa and India by studies on other taxa (Warren et al. 2010; Condamine et al. 2013).

Regarding the falcons lineage, their ancestor underwent a extinction of lineages in evergreen tropical forests and a subsequent radiation and ecological specialization during the middle and late Miocene associated with open habitats (Fuchs et al. 2015). In this context, the reconstructed scenario and the biome occupation tendencies are in concordance with the increase of open, dry and seasonal environments and shrinkage of rainforest (Jacobs 2004; Senut et al. 2009; Edwards et al. 2010). The phylogeny presents a divergence event between the *Falco* lineage and *Polihierax insignis* during the middle Miocene. The extant Indochinese presence of *P. insignis* may suggest a scenario where *Microhierax* ancestors and *P. insignis* dispersed from Africa and colonized Asia independently. This agree with previous notions of an Asian or African origin for *Falco* (Olson 1985; Becker 1987; Boev 2011; Fuchs et al. 2015). This process could have taken place through the stepping stones connection (Yoder and Nowak 2006; Warren et al. 2010) or across the land bridge that enabled the *Conohyus/Pliopithecus* event, with many Eurasian taxa entering in Africa around 14 Ma (van der Made 1999). The presence of tropical deciduous woodlands and savannas in the Middle East during this period (Edwards et al. 2010; Pound et al. 2012) might have propitiated this expansion towards Asia.

Middle Miocene *Falco* ancestors were associated with tropical deciduous woodlands and savannas and presented a subsequent radiation in the late Miocene. The fossil record evidences a broad distribution of *Falco* in Eurasia since the middle and late Miocene (Mlíkovský 1996, 2002; Boev 2011; Li et al. 2014) and crossed to North America through Beringia (Becker 1987). Both continents, especially the eastern Mediterranean, western-central Asia and the Great Plains underwent a profound ecological transformation with the expansion of C4 grasses in open, dry and seasonal environments, associated to climate changes and variations in the CO₂ levels (Cerling et al. 1993; Wang et al. 1994; Latorre et al. 1997; Edwards et al. 2010; Strömberg and McInerney 2011; Fraser and Theodor 2013). There are evidences of

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Falco bulgaricus, from late Miocene Bulgaria associated to typical tropical deciduous woodland and savanna megafauna (Boev 2011). *Falco hezhengensis*, from late Miocene central Asia (China), included jerboa (Dipodidae) in its diet, indicating their presence in transitional savanna-steppe grasslands (Li et al. 2014).

Our results suggest that *Falco* diversification during the late Miocene into two main lineages: the *F. zoniventris*-group and the *F. sparverius*-group was in close association with open, dry and seasonal biomes such tropical deciduous woodland and savannas. During this period, the spread of open environments (Cerling et al. 1993) coincided also with the diversification of many rodents groups (Smith and Patton 1999; Galewski et al. 2006; Lecompte et al. 2008; Fabre et al. 2012), an important feeding source of falcons. Considering the *Falco zoniventris*-group, the close association with the savanna biome is consistent with the African scenario proposed for the evolution of this clade (Groombridge et al. 2002). Also, it would have been concomitant with an important increase of aridity in Africa during the Plio-Pleistocene, which culminated with the development of the Sahara desert (Hernandez Fernandez et al. 2007; Senut et al. 2009).

The phylogeny and the geographic distribution for the *Falco sparverius*-group suggest a biogeographic scenario with multiple biome colonization events between Eurasia and North America, and subsequent peripheral dispersal events towards Africa, Australia and South America. These interchanges are consistent with sea level fluctuations during the glacial periods and the establishment of land bridges such as Beringia, or biotic interchange events as the Elephant-*Equus* or *Pachycrocuta* (Sanmartín et al. 2001; Nores 2004; Martínez-Navarro 2010; DiNezio and Tierney 2013).

Overall, the diversification of kestrels and falcons in relation to the obtained patterns of biomes colonization may suggest that the initial development of a high flight capacity associated with seasonally environments by Falconini ancestors might had an important role as exaptation (Gould and Vrba 1982) for the ulterior independent development of a true migration behaviour in many falcon lineages (Rolland et al. 2014; Fuchs et al. 2015). This feature explains the dispersal capacity of this clade and the relatively frequent colonization of adverse environments such as deserts, steppes or tundras (Pelegrin et al. 2015) where these lineages show a high level of conservatism. The ancestral development of a wide spectrum of feeding and

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physiological adaptations, such as tolerance to high body temperatures and the low water dependency related to their carnivorous habits (Bartholomew and Cade 1957; Masman et al. 1989) might have evolved in savanna-like conditions and enabled the adaptation to the dryer climatic environments of the recently appeared deserts and steppes consolidated in the Northern Hemisphere during the Pleistocene (Fine and Ree 2006). According to our findings these relatively recent biomes and others such as sclerophyllous woodland-shrubland and the expanding taiga were colonized by relatively young lineages, which is consistent with the speciation patterns observed for many Holarctic vertebrate clades during the Pleistocene ice-ages (Hewitt 2000; Weir and Schluter 2004).

4.5.3. *Patterns of biome colonization in Galliformes and Falconiformes*

Along the time the results for Galliformes suggest different phases of biome colonization (Fig.4), during the early Oligocene the tropical deciduous woodland and the temperate evergreen forest presented an outstanding growing. Probably these results are related with the global cooling trend (Zachos et al. 2001) that affected the extension of tropical evergreen forest zones causing its fragmentation and contraction. These processes would have promoted the colonization of emerging habitats in drier tropical deciduous woodlands and temperate evergreen forests in northern latitudes (Collinson and Hooker 2003). Around the Oligocene-Miocene boundary, the savanna registered an increase of colonizations reaching a maximum value during the early Miocene, which is consistent with the early replacement of grassland biomes that began to supplant forestlands (Jacobs 2004; Edwards et al. 2010). Likewise, the savannas experimented a second colonization increase during late Miocene and Pliocene, in line with the worldwide expansion of C4 grasslands, event that possibly generated new savannas environments (Cerling et al. 1993; Bouchenak-Khelladi and Hodkinson 2011). During the early Miocene the broadleaf deciduous forest biome presented an increase of colonizations. This process might be related to the ecological gradient established by the initial Himalayan uplift (Shi et al. 1999; Miao et al. 2012; Guo et al. 2008), which affected significantly the evolution of Phasianidae lineages in Asia. There was a marked growth in the colonization rates for the majority of biomes in the middle and late Miocene times. After the Mid-Miocene Climate Optimum, the global decreasing in temperatures generated tendencies towards cooling and aridification that intensified the emergence of

seasonal biomes. Likewise, biomes such as the evergreen tropical rainforest presented a significant reduction and fragmentation. According to this, our findings showed an important increase in colonization rates for this biome. The patterns observed for evergreen tropical rainforest suggest that contractions probably promoted the colonization events of many tropical lineages by dispersal events from proximal biomes toward diverse rainforest blocks consolidating the early endemism areas (Cracraft 1985) during the middle and late Miocene. Thus, Plio-Pleistocene rainforests would have subsequently acted such as refugia for many lineages during cooler periods. This would have promoted vicariance according to our findings and other studies based on rainforest faunas (Haffer 2008; Bennett et al. 2012). Since the late Miocene the seasonal biomes presented a progressive pattern of expansion, until their consolidation in the Pleistocene. Probably expansion in biomes such as deserts (Senut et al. 2009), steppes (Miao et al. 2012; Humphreys and Linder 2013), taigas (Pound et al. 2011) and sclerophyllous woodland-shrublands (Hernandez Fernandez et al. 2007) might facilitate the novel emergency of ecological niches, which made possible the increasing observed in the colonization patterns for these environments until the Plio-Pleistocene. Likewise, with the glacial-interglacial alternancy, whereas a few lineages adapted to tundra biomes, many of these biomes were important refugia areas of endemism for many lineages with climatic constraints (Hewitt 2000; Weir and Schluter 2004; Abellán and Svenning 2014; An et al. 2015).

Our findings for Falconiformes (Fig.5) suggest that during the Oligocene only the temperate evergreen forest was colonized, this biome would appeared during the initial uplift phases of Andes uplift (Hoorn et al. 2010). The observed pattern probably has relation with the basal evolution of Falconiformes restricted to South America where they probably occupied a broad spectrum of tropical biomes. Interestingly, conserving the tropical affinities along their early diversification. During the middle Miocene the falcons presented a significant increase of colonization processes in evergreen tropical forest and deciduous woodland biomes as well as temperate evergreen forest in the mountains (Hoorn et al. 2010). During this period, the intense uplift process of Andes caused the continuous fragmentation in the tropical forest biomes (Wesselingh and Salo 2006) and the arising of new ecological niches and vicariance scenarios in Neotropic lowlands (Valderrama et al. 2014).

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The colonization of more arid biomes took place during the late Miocene. This timing fit the colonization reported for Galliformes and is probably connected to the global cooling that followed the Mid-Miocene Climate Optimum (Zachos et al. 2001; van Dam 2006; Liu et al. 2009; Senut et al. 2009). Moreover, the diversification of falconids out of South America probably increased the possibility of colonizing new environments. According to this, the results showed an increase during the late Miocene in colonization for semi-open biomes such as tropical deciduous woodlands and sclerophyllous woodland-shrubland as well as open biomes such as deserts, savannas and steppes. All these findings are consistent with fossil evidences (Boev 2011; Li et al. 2014). During this period, these seasonal biomes expanded their distribution towards high latitudes and open environments acquired an especial ecological relevance (Bredenkamp et al. 2002; Edwards et al. 2010; Cerling et al. 1993). Likewise, during the late Miocene and Pliocene, the falconids also showed an increase of colonizations of temperate and high latitudes biomes such as broadleaf deciduous forest, boreal coniferous forest and tundra. These patterns support the previous development of different physiological traits (Klaassen 1996) and a high dispersal flight (Thorup 2006), probably linked to the evolution of migration, which made possible the dispersal into diverse environments (Rolland et al. 2014; Pelegrin et al. 2015). These factors could explain the observed similarity in the colonization patterns for diverse biomes at the same time and the diverse trends towards a significant presence of basal lineages in warm tropical biomes while the subtropical, temperate latitudes and cool or dry biomes in tropical ones were colonized by more derived lineages in subsequent times. These findings are broadly consistent with analyses of the relationship between niche conservatism and latitudinal diversity gradient in birds (Hawkins et al. 2006).

4.5.4. Trends in phylogenetic biome conservatism

The results obtained for the biome colonization patterns in Galliformes and Falconiformes (Figures 3, 6) revealed high levels of phylogenetic conservatism of biome (%BC) for landfowls and falcons. Biome occupancy was conserved along the phylogeny of Galliformes in 475 of 767 (61.92%) transition events while the colonizations were represented by 292 events (38.08%) (Table 2, Fig.3). For each biome the findings support BC values higher than 50%, except the savanna and sclerophyllous woodland-shrubland. Interestingly, biomes in the extreme of climatic

gradient consistently presented BC values above 75%: evergreen tropical rainforest (82.93%), steppe (83.78%) and tundra (100%). Meanwhile, Falconiformes also presented a high biome conservatism values with a similar proportion respect to Galliformes. The BC for Falconiformes was represented in 273 of 436 (62.61%) possible biome transitions while resting 37.39% are represented by 163 new biome colonizations (Table 3, Fig.6). Likewise, highest score values were registered for evergreen tropical rainforest (82.5%), steppe (77.8%), taiga (93.8%), and tundra (87.5%). In a broad view, despite their more generalist biome occupancy, the biome conservatism is strong in both Falconiformes and Galliformes. These similarities suggest common triggering processes such as abiotic changes. Such events would have mainly affected extreme biomes with the relative recent colonization of emerging steppes, taigas and tundras. The development of physiological adaptations to cold environments (McNab 2009) probably constitutes like constraints for subsequent colonizations (Hawkins et al. 2007). Likewise, the historical high resources availability and heterogeneity of habitats in tropical rainforest biome may constitute important factors promoting biome conservatism (Hawkins et al. 2003; Wiens 2004; Peterson and Nyari 2008) resulting in the existence of rainforest lineages since the Eocene and Oligocene.

Taken together, our findings depict both the tropical deciduous forests and the savannas as significant evolutionary arenas for both bird groups (Figures 3, 6). The significant biome colonization rates related to these biomes reveal their importance acting as possible species cradle and corridor. Due to their seasonal and thermic intermediate conditions (Pennington et al. 2006), these biomes might presented a broad spectrum of environmental variations, thus the species adaptation to seasonal and dry conditions of these biomes would have promoted the development of a broad physiological spectrum to cope such diverse environmental variations. This trend would have consolidated these biomes as species cradle. In this way, the wide adaptive spectrum allows the gradual colonization and subsequent specialization to the climatic condition of extreme biomes such as desert (Guerrero et al. 2013; Jara-Arancio et al. 2014). Under this context, bird evolutionary success might have resulted not by continuous adaptation to new environments but from the development of a broad adaptive physiological spectrum by particular lineages in seasonal biomes that would allowed the expansion and dispersal capacity to colonize areas with similar climatic conditions during climatic and geologic changes. In

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particular, our work emphasizes the evolutionary importance of the tropical deciduous woodland in bird evolution. Despite the strong phylogenetic conservatism of savanna-adapted lineages, this biome represents an important connector between tropical and temperate biomes consoling a source of species for other biomes.

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Appendix 4.8.



4. Phylogeny and biome occupancy

Appendix 4.8.1. Table S1. Biome existence matrix

Table S1A. Since Pliocene-Pleistocene

Source	I	II	II/III	III	IV	V	VI	VII	VIII	IX
I	1	1	1	0	0	1	0	0	0	0
II	1	1	1	1	1	1	1	1	0	0
II/III	1	1	1	1	1	1	1	1	0	0
III	0	1	1	1	1	0	1	1	1	0
IV	0	1	1	1	1	1	1	1	1	0
V	1	1	1	0	1	1	1	0	1	0
VI	0	1	1	1	1	1	1	1	1	1
VII	0	1	1	1	1	0	1	1	1	1
VIII	0	0	0	1	1	1	1	1	1	1
IX	0	0	0	0	0	0	1	1	1	1

Table S1B. During Oligocene and Miocene

Source	I	II	II/III	III	IV	V	VI	VII	VIII	IX
I	1	1	1	0	0	1	0	0	0	0
II	1	1	1	0	0	1	1	0	0	0
II/III	1	1	1	0	0	1	1	0	0	0
III	0	0	0	0	0	0	0	0	0	0
IV	0	1	1	0	0	1	1	0	1	0
V	1	1	1	0	0	1	1	0	1	0
VI	0	1	1	0	0	1	1	0	1	0
VII	0	0	0	0	0	0	0	0	0	0
VIII	0	0	0	0	0	1	1	0	1	0
IX	0	0	0	0	0	0	0	0	0	0

Appendix 4.8.2. Table S2. 239 diverse biome occupation of non-passerine birds.

[1]]	[[21]]	[[41]]	[[61]]	[[81]]	[[101]]	[[121]]
I	VI VIII	II/III IV V	I II/III V	V VI VII VIII	II II/III IV VII	II V VI VIII
[[2]]	[[22]]	[[42]]	[[62]]	[[82]]	[[102]]	[[122]]
II	VI IX	VI VII VIII	III VII VIII	II IV VI VII	I II V VI	III IV V VII
[[3]]	[[23]]	[[43]]	[[63]]	[[83]]	[[103]]	[[123]]
IV	VII IX	II II/III III	I IV V	II II/III III IV	I II II/III IV	I II II/III IV V
[[4]]	[[24]]	[[44]]	[[64]]	[[84]]	[[104]]	[[124]]
VII	VII VIII	IV V VII	III VI VII	I II II/III III	V VI VII IX	II II/III III IV V
[[5]]	[[25]]	[[45]]	[[65]]	[[85]]	[[105]]	[[125]]
II/III	IV VII	V VI VIII	II IV VI	III IV V VI	II/III III IV VII	IV V VI VII VIII
[[6]]	[[26]]	[[46]]	[[66]]	[[86]]	[[106]]	[[126]]
IX	V VIII	V VI VII	III IV VI	IV V VII VIII	IV VI VIII IX	I II/III V VII VIII
[[7]]	[[27]]	[[47]]	[[67]]	[[87]]	[[107]]	[[127]]
V	IV V	II II/III IV	I II IV	III IV VI VII	II II/III VI VII	I II II/III V VIII
[[8]]	[[28]]	[[48]]	[[68]]	[[88]]	[[108]]	[[128]]
VIII	V VII	V VI IX	I V VII	II/III III IV V	III IV VI IX	II II/III III V VIII
[[9]]	[[29]]	[[49]]	[[69]]	[[89]]	[[109]]	[[129]]
VI	II III	IV V VI	II/III V VIII	IV VI VII VIII	I II III IV	I II IV V VI
[[10]]	[[30]]	[[50]]	[[70]]	[[90]]	[[110]]	[[130]]
III	I II/III	VI VIII IX	IV VI VIII	II II/III IV V	II V VI VII	II II/III V VII VIII
[[11]]	[[31]]	[[51]]	[[71]]	[[91]]	[[111]]	[[131]]
I V	III IV	VII VIII IX	II/III III VII	VI VII VIII IX	I II IV V	III V VI VIII IX
[[12]]	[[32]]	[[52]]	[[72]]	[[92]]	[[112]]	[[132]]
I II	II/III VII	II/III III IV	II IV V	I II V VII	II II/III V VII	I II II/III III V
[[13]]	[[33]]	[[53]]	[[73]]	[[93]]	[[113]]	[[133]]
II II/III	II VII	VI VII IX	II II/III 7	I V VII VIII	II II/III V VI	I II VI VII VIII
[[14]]	[[34]]	[[54]]	[[74]]	[[94]]	[[114]]	[[134]]
II V	II VI	II III V	II III IV	II IV V VI	II II/III III V	II/III III V VI VII
[[15]]	[[35]]	[[55]]	[[75]]	[[95]]	[[115]]	[[135]]
VI VII	II/III V	V VII VIII	I II III	IV V VI VII	III VI VII VIII	II II/III III IV VII
[[16]]	[[36]]	[[56]]	[[76]]	[[96]]	[[116]]	[[136]]
V VI	IV VI VII	I V VIII	II/III VI IX	I II III V	I II II/III VII	I II II/III VII VIII
[[17]]	[[37]]	[[57]]	[[77]]	[[97]]	[[117]]	[[137]]
II/III IV	I II V	II V VIII	II/III IV VII	I II V VIII	IV V VII IX	I IV V VI VII
[[18]]	[[38]]	[[58]]	[[78]]	[[98]]	[[118]]	[[138]]
IV VI	I II II/III	II III VII	II/III III VI	II II/III V VIII	V VI VIII IX	IV VI VII VIII IX
[[19]]	[[39]]	[[59]]	[[79]]	[[99]]	[[119]]	[[139]]
II/III 3	II II/III V	III IV VII	II VII VIII	II/III III IV VI	II III V VIII	II/III IV V VI VII
[[20]]	[[40]]	[[60]]	[[80]]	[[100]]	[[120]]	[[140]]
VIII IX	I V VI	II V VI	I II II/III V	II V VII VIII	IV V VI VIII	I III IV V VI

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[[141]]	[[161]]	[[181]]	[[201]]	[[221]]
V VI VII VIII IX	I II V VI VII	I II IV V VI VII	I II II/III III IV V VII	II II/III III IV V VII VIII
[[142]]	[[162]]	[[182]]	[[202]]	[[222]]
I II V VII VIII	II IV V VII VIII	IV V VI VII VIII IX	II/III III IV V VI VII VIII	II III V VI VII VIII IX
[[143]]	[[163]]	[[183]]	[[203]]	[[223]]
II V VI VII VIII	II II/III III V VII	I II III IV V VI	I II II/III V VI VII VIII	II/III III IV V VI VII VIII IX
[[144]]	[[164]]	[[184]]	[[204]]	[[224]]
II/III III IV VI VII	II V VI VII IX	I II II/III V VI VII	I II V VI VII VIII IX	II III IV V VI VII VIII IX
[[145]]	[[165]]	[[185]]	[[205]]	[[225]]
III IV V VI VII	IV V VI VIII IX	II II/III IV V VII VIII	III IV V VI VII VIII IX	I II II/III III IV V VI VII
[[146]]	[[166]]	[[186]]	[[206]]	[[226]]
I II III V VI	I II V VI VIII	II/III III V VI VII IX	II/III III IV VI VII VIII IX	I II II/III V VI VII VIII IX
[[147]]	[[167]]	[[187]]	[[207]]	[[227]]
II/III V VI VII IX	I II II/III IV V VI	I II IV VI VII VIII	I II II/III III IV V VI	I II II/III III IV V VII VIII
[[148]]	[[168]]	[[188]]	[[208]]	[[228]]
I II/III IV V VII	II/III III IV V VI VII	III IV VI VII VIII IX	II II/III III IV V VI VII	I II III IV V VI VII VIII
[[149]]	[[169]]	[[189]]	[[209]]	[[229]]
II II/III IV V VI	II II/III III IV V VI	I II V VI VII VIII	I II/III IV V VI VII VIII	II II/III IV V VI VII VIII IX
[[150]]	[[170]]	[[190]]	[[210]]	[[230]]
II II/III III IV VI	II/III IV V VI VII VIII	II II/III V VI VII VIII	II II/III IV V VI VII VIII	I II II/III IV V VI VII VIII
[[151]]	[[171]]	[[191]]	[[211]]	[[231]]
I II II/III III IV	II II/III III V VII VIII	II II/III IV V VI VII	I II III IV V VI VII	II II/III III IV V VI VII VIII
[[152]]	[[172]]	[[192]]	[[212]]	[[232]]
I II II/III V VI	II II/III III IV VI VII	II III IV VI VII VIII	II II/III III V VI VII VIII	I II II/III III IV VI VII VIII
[[153]]	[[173]]	[[193]]	[[213]]	[[233]]
II II/III V VI VII	I II II/III V VII VIII	II IV V VI VII VIII	I II II/III IV V VI VII	I II II/III III V VI VII VIII
[[154]]	[[174]]	[[194]]	[[214]]	[[234]]
II/III III IV V VI	I II II/III III IV V	I II II/III IV V VIII	I II/III III IV V VI VII	II II/III III IV V VI VII IX
[[155]]	[[175]]	[[195]]	[[215]]	[[235]]
I V VI VII VIII	I II II/III III IV VII	II II/III IV VI VII VIII	I II II/III III V VII VIII	II II/III III V VI VII VIII IX
[[156]]	[[176]]	[[196]]	[[216]]	[[236]]
I II II/III V VII	II/III III IV VI VII VIII	I IV V VI VII VIII	I II II/III IV V VI VIII	I II II/III III IV V VI VII VIII
[[157]]	[[177]]	[[197]]	[[217]]	[[237]]
II III IV V VI	II II/III III IV V VII	I II II/III III V VI	I II II/III IV VI VII VIII	I II II/III III IV V VI VII IX
[[158]]	[[178]]	[[198]]	[[218]]	[[238]]
III IV VI VII VIII	I II II/III 6 VII VIII	II II/III IV V VI VIII	II III IV V VI VII VIII	II II/III III IV V VI VII VIII IX
[[159]]	[[179]]	[[199]]	[[219]]	[[239]]
II II/III III VI VII	I V VI VII VIII IX	II IV VI VII VIII IX	I II II/III III IV V VIII	I II II/III III IV V VI VII VIII IX
[[160]]	[[180]]	[[200]]	[[220]]	
II II/III IV V VII	III IV V VI VII VIII	II IV V VI VIII IX	I II II/III III IV VI VII VIII	

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Appendix 4.8.3. Table S3. Biomes definition for each node in Galliformes based in probability values for each node. (I= Tropical rain forest; II= Tropical deciduous woodland; II/III= Savanna; III= Subtropical Desert ; IV= Sclerophyllous woodland-shrubland; V=Temperate evergreen forest; VI=Temperate broadleaf deciduous forest; VII= Steppe to cold desert; VIII=Boreal coniferous forest (Taiga);IX=Tundra).

Node	Probability of combinations until (50%)	Defined biomes
1	II/III=3.96; II,II/III=3.82; II=3.68; I,II,II/III=3.54; I,II/III=3.54 II,II/III,V=3.49; I,II,II/III,V=3.40; II/III,V=3.40; I,II=3.38; II,V=3.27; II,II/III,V,VI=3.25; I II II/III V VI=3.24; I,II/III,V=3.23; I II V=3.15; I,II,V,VI=3.01	I, II, II/III,V
2	II=14.02; II/III=12.88; V=10.41; VI=7.47; VIII=4.22; II,II/III=3.83	Indet.
3	II=20.81; II/III=19.94; II,II/III=6.57; V=6.45	II, II/III
4	II/III=29.74; II=25.61	II/III, II
5	II/III=28.25; II=20.67; V=9.42	II/III
6	II/III=35.45; II=22.34	II/III
7	V=32.89; I,V=24.42	V
8	II=34.74; I,II=16.66	II
9	II=64.98	II
10	II=61.85	II
11	II=49.15; I,II=25.93	II, I
12	I,II=40.66; II=26.84	II, I
13	II=54.47	II
14	I,II=45.46; II=28.50	II, I
15	I,II=45.86; II=29.60;	I, II
16	I,II=48.49; II=40.04	I,II
17	II,V=17.52; V=17.44; II=11.89; I,II,V=9.02	II, V
18	V=58.47	V
19	V=81.46	V
20	V=74.45	V
21	V=60.15	V
22	V=51.78	V
23	V=79.98	V
24	I,V=33.66; V=25.08	I,V
25	I,II,V=66.40	I, II, V
26	II=58.14	II
27	I, II=59.95	I, II
28	V=76.02	V
29	V=26.64; I,V=19.06; I,II/III,V=10.15	I, V
30	V=74.05	V
31	V=58.25	V
32	II=39.94; V=16.56	II
33	II=65.45	II
34	II=58.27	II
35	II=48.97; I,II=24.59	II
36	II=49.85; II,V=20.35	II
37	II=55.89	II
38	II=56.60	II
39	I,II=70.19	I, II
40	II=59.83	II
41	II=72.01	II
42	II=69.11	II
43	II=84.70	II
44	II=73.15	II
45	II=61.38	II

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46	I,II=86.52	I, II
47	II=66.53	II
48	II=83.13	II
49	II=50.10	II
50	II=85.51	II
51	II=93.60	II
52	II=47.81; I, II=37.32	II, I
53	II=93.74	II
54	I, II=34.46; II=33.57	II, I
55	II=23.31; II/III=12.76; V=7.29; II,II/III=5.44; VI=5.42	II
56	II/III=28.42; II=16.33; I,II/III=7.36	II/III
57	II/III=39.11; II=23.32	II/III
58	I,II/III=20.76; II/III=17.91; I,II=12.60	I, II/III
59	II/III=36.91; II=22.63	II/III
60	II=34.53; II/III=14.56; V=9.35	II
61	II=22.32; II/III=14.32; V=9.56; VI=7.35	Indet.
62	II/III=19.76; II=18.44; I, II/III=10.35	II/III
63	V=15.58; II=11.64; VI=11.57; II/III=5.19; II;V=4.48; V,VI=4.34	Indet.
64	V=26.76; VI=10.19; II=9.23;VIII=5.14	V
65	V=40.49; I,V=13.07	V
66	V=33.41; I,V=15.23; II=10.21	V
67	I,V=40.87; V=28.53	I, V
68	II=15.38; VI=15.33; V=11.09; II/III=7.34; II,VI=7.06	Indet.
69	II=22.66; II/III=12.33; VI=5.28; II,VI=4.64; II,II/III=4.64; I,II=3.27	II
70	II,II/III,V,VI=17.93; II=7.99; II,II/III,V=7.43; I,II=6.40; II,II/III=6.13; I, II,II/III=6.05	II,II/III,V
71	II,III=9.16; II/III=8.74; II=8.64; III=8.37; II/III,III=4.64; II,VII=3.68; II,II/III,III=3.39	II, III
72	II=14.93; II/III=11.25; III=10.58; II,II/III=9.21; II,III=8.50	II
73	III=21.42; III,IV=13.26; III,IV,VII=12.73; III,VI,VII=11.40	III, IV
74	II=41.09; II/III=9.93	II
75	II=33.07; II/III=12.94; V=7.53	II
76	II,V=70.75	II, V
77	II=31.81; V=13.67; II/III=7.89	II
78	II=27.20; V=13.19; II,V=8.37; I,II=8.11	II
79	V=29.65; I,V=21.00	V
80	II=46.85; I,II=17.31	II
81	II=50.87	II
82	II=58.87	II
83	II=29.93; II/III=10.59; V=9.17; I,II=7.00	II
84	II=48.00; II;VI=7.18	II
85	II=43.48; II/III=11.66	II
86	II=31.37; II/III=15.66; II,II/III=6.71	II
87	II=35.15; II/III=17.37	II
88	II=25.21; II/III=18.04; II,II/III=7.26	II
89	II=21.92; II/III=18.45; II,II/III=5.76; II,V=3.08; V=2.80	II
90	II,II/III,IV,V,VI,VII,VIII=31.76; II,II/III,IV,V,VI,VIII=8.58; II,II/III,V,VI,VII,VIII=7.74; II,II/III,IV,V,VI,VII=7.41	II,II/III,IV,V,VI,VII,VIII
91	II=15.84; II/III=12.54; V=9.18; II,II/III=4.79; II,V=4.51; I,II=4.48	II
92	II,II/III,III,IV,V,VI=23.22; II,III,IV,V,VI=6.33; II,II/III,III,IV,V=6.12; II,II/III,IV,V,VI=6.02; I,II,V,VII,VIII=5.82; II,II/III,III,IV,V,VI,VII=4.85	II,II/III,III,IV,V,VI
93	II=48.13; II/III=15.25	II
94	II=15.36; II/III=11.57; II,VII=10.72; VII=8.38; II/III,VII=7.75	II, VII
95	VII=77.44	VII

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96	VII=93.12	VII
97	II=49.87; II/III=16.56	II
98	VI=31.50; II=16.56; II,VI=14.38	VI, II
99	VI=29.39; II=19.17; II,VI=12.92	VI, II
100	VI=36.53, VII=8.62; IV=6.52	VI
101	VI=42.08; VII=11.21	VI
102	VI,VII=24.68; VI=20.25; VII=17.03	VI, VII
103	VII=76.53	VII
104	II=47.95; II/III=19.56	II
105	II=36.76; II/III=24.24	II
106	II=41.00; II/III=13.77	II
107	II=44.38; II,V=13.77	II
108	II=80.99	II
109	II=85.46	II
110	II=53.69	II
111	I,II=43.54; II=34.30	I,II
112	II=91.78	II
113	II=74.55	II
114	II=53.40	II
115	II=39.18; II/III=23.39	II
116	II=35.73; II,II/III=20.27	II
117	II=84.56	II
118	II=28.83; II,V=28.70	II, V
119	II=90.60	II
120	II=74.01	II
121	II=80.64	II
122	II=27.47; V=18.60; II,V=11.01	II, V
123	V=29.58; I,V=17.13; II=7.75	V
124	II=15.28; V=12.68; II,V=7.72; II/III,V=3.08; II,III,V=3.00; II/III=2.76; II,II/III,V=2.63; II,V,VIII=2.60; II,II/III=2.56	V, II
125	II,III,V=15.90; II,III,V,VIII=12.10; II,V=8.98; II/III,V=7.31; II,III=5.64; IV,V=4.79	V, II, III,
126	II=46.09; II, VI=15.77	II
127	II=63.89	II
128	II=48.65; I,II=8.73	II
129	II=41.42; II/III=14.45	II
130	II=69.89	II
131	II=69.24	II
132	II=84.04	II
133	II=84.67	II
134	II=73.58	II
135	I,II=56.86	I, II
136	I,II=31.64; II=31.29	I, II
137	II=65.75	II
138	II=55.59	II
139	II=30.66; I,II=19.55	II
140	II=43.85; I,II=24.50	II
141	II=40.27; I,II=11.05	II
142	II=70.08	II
143	II=64.63	II
144	II=47.17; I,II=13.22	II
145	II=44.67; I,II=18.76	II
146	II=59.12	II
147	I,II,V=62.59	I, II, V
148	II=80.64	II

4. Phylogeny and biome occupancy

149	II=66.13	II
150	II=17.93; II/III=15.58; II, II/III=8.66; II,II/III,IV=3.25; II,II/III,III=2.73; II,II/III,VII=2.59	II, II/III
151	II=59.59	II
152	II=50.75	II
153	II=77.84	II
154	II=81.98	II
155	II=75.97	II
156	II=82.00	II
157	II=73.55	II
158	II=79.54	II
159	II=55.31	II
160	II=70.58	II
161	II=47.75; II,VIII=10.35	II
162	II=28.52; II, II/III=20.21; II/III=17.07	II, II/III
163	II/III=45.30; II,II/III=17.72	II/III
164	VI=30.61; II=17.18; II,VI=14.90	VI, II
165	VI=45.20; V=9.24	VI
166	VI=42.22; VIII=12.76;	VI
167	V=56.58	V
168	V=66.07	V
169	V=61.92	V
170	VI=38.25; VIII=25.02	VI, VIII
171	VI=44.47; VI,VII=17.32	VI
172	VII,VIII=30.29; VIII=30.23	VIII, VII
173	VII=56.41	VII
174	VI=52.19	VI
175	VI=41.77; VIII=14.01	VI
176	II=12.20; II,V=4.26; I,II=4.11; II,VI=3.87; II,II/III,V,VI=3.54; II,V,VI=3.45; II,II/III,V=2.32; V=2.29; II,II/III=2.17; I,II,V=2.05; II,IV,V=1.87; II,IV,V,VI=1.86; II,II/III,IV,V,VI=1.80; II,V,VI,VII=1.72; II,II/III,IV,V,VI,VII=1.65; I,II,II/III,V,VI=1.54	II, V
177	VIII=39.48; VI=26.52	VIII, VI
178	VI=51.38	VI
179	VIII=61.16	VIII
180	VIII=81.48	VIII
181	VIII=85.42	VIII
182	VIII=87.78	VIII
183	VIII=60.88	VIII
184	VI,VII=15.10; VII,VIII=14.71; VI=13.75; VI,VII,VIII=12.76	VI, VII, VII
185	VIII=54.04	VIII
186	VIII=91.62	VIII
187	VIII=97.98	VIII
188	VIII=61.75	VIII
189	VII=88.66	VII
190	VIII=41.92; VI=17.70	VIII
191	VI,VIII=45.64; VI=40.97	VI, VIII
192	VI,VII,VIII=41.49; VI,VII=20.28	VI, VII,VIII
193	VI,VII,VIII=50.83	VI, VII,VIII
194	VIII=69.27	VIII
195	VIII, IX=25.18; IX=24.16; VIII=23.84	VIII, IX
196	VI,VIII,IX=54.65	VI,VIII,IX
197	VI=51.98	VI
198	VI=28.02; V=11.65; II=9.23; II, VI=7.69	VI
199	VI=51.94	VI

4. Phylogeny and biome occupancy

200	VII=26.77; VI=20.24; VI,VII=15.03	VII, VI
201	VII=34.52; VI=32.69	VII, VI
202	VI=35.98; V=14.22	VI
203	V=30.67; VI=25.68	V, VI
204	V=43.06; VI=22.36	V
205	V=69.37	V
206	II,V=50.48	II, V
207	VI=33.49; II=18.17	VI
208	V,VI=19.03; II,V,VI=17.45; VI=15.53	VI, V
209	VI=14.00; V,VI=11.94; II,V,VI,VII=10.42; II,V,VI=9.26; V=7.31	VI, V
210	VI=34.26; II=31.45	VI, II
211	II=41.65; VI=22.10	II
212	VII=43.33; VI,VIII=7.97	VII
213	VII=33.38; VII,VIII=13.27; V,VI,VII,VIII=9.65	VII
214	VI,VII=92.12	VI,VII
215	II=54.89	II
216	II=64.34	II
217	II=65.88	II
218	II=69.52	II
219	II=85.82	II
220	I,II=46.97; II=42.45	I, II
221	II=99.74	II
222	II=50.95	II
223	II=68.89	II
224	II=81.53	II

4. Phylogeny and biome occupancy

Appendix 4.8.4. Table S4. Biomes definition for each node in Falconiformes based in probability values for each node. (I= Tropical rain forest; II= Tropical deciduous woodland; II/III= Savanna; III= Subtropical Desert ; IV= Sclerophyllous woodland-shrubland; V=Temperate evergreen forest; VI=Temperate broadleaf deciduous forest; VII= Steppe to cold desert; VIII=Boreal coniferous forest (Taiga);IX=Tundra).

Node	Probability of combinations until (50%)	Defined biomes
1	II/III=5.11; I,II/III=5.03; II,II/III=4.79; I,II,II/III=4.66; I,II/III,V=4.08; II/III,V=4.02; I,II,II/III,V=3.96; I,II=3.95; II,II/III,V=3.39; II=3.75; I,II,V=3.37	I,II,II/III
2	II/III=9.65; I,II,II/III,V,VI=8.57; I,II,II/III,V=7.13; I,II,II/III=5.62; II=5.30; II,II/III=5.11; I,II/III=4.60; I,II/III,V=4.38	I,II,II/III
3	I,II,II/III,V,VI= I,II,II/III,V= II/III= I,II,II/III= II,II/III,V,VI= I,II/III,V= I,II,II/III,V,VIII= I,II/III=	I, II, II/III, V
4	I,II,II/III,V=10.16; I,II,II/III=9.74; I,II,II/III,V,VI=7.40; II=6.56; II/III=6.53; I,II=6.43; I,II/III=6.10	I, II, II/III
5	I,II=15.09; I,II/III=13.10; I,II,II/III=11.22; I,II/III,V=10.24; I,II,V=7.28	I, II, II/III
6	I,II=16.54; II=16.28; I,II,II/III=8.58; I,II,V=6.44; I,II,II/III,V=6.24	I, II
7	I,II=28.26; I,II,II/III=12.76; I,II,V=8.83; I,II,II/III,V=7.75	I, II
8	II=30.50; I,II=25.09	I, II
9	II=26.01; I,II=18.20; I,II,II/III=6.48	II
10	II/III=12.14; I,II,II/III,V,VI=7.67; I,II,II/III,V=6.41; II=5.69; I,II,II/III=5.45; II,II/III=5.39; I,II/III=4.96; I,II/III,V=4.41	I, II, II/III
11	I,II,II/III,V,VI=17.83; I,II,II/III,V=10.03; II,II/III,V,VI=6.87; I,II,II/III,V,VIII=5.77; I,II,II/III=5.41; II/III=3.90; I,II/III,V=3.81	I, II, II/III, V
12	I,II,II/III,III,IV,V,VI,VII,VIII=34.32; I,II,II/III,IV,V,VI,VII,VIII=8.96; I,II,II/III,III,IV,V,VI,VII=8.48	I,II,II/III,III,IV,V,VI,VII,VIII
13	II/III=18.89; II=14.69; II,II/III=7.21; I,II/III=6.74; I,II,II/III=5.78	II, II/III
14	II=6.53; I,II=4.05; II/III=3.55; I,II/III=3.33; II,VI=2.64; I,II,II/III,VII=2.51; I,II,II/III=2.32; I,II/III,V=2.24; II,II/III=1.73; II,VII=1.68; I,II,II/III,V=1.56; V=1.53; II,II/III,IV,V,VI,VII=1.48; II,II/III,VII=1.47; VI=1.36; II,V,VI=1.26; I,II,II/III,V,VI=1.26; II,IV,VI=1.21; II,IV,VI,VII=1.21; II,II/III,III,IV,V,VI,VII=1.20; II,II/III,III,IV,V,VI=1.17; II/III,V=1.16; I,II,V=1.15; II/III,VII=1.14; I,II,II/III,V,VII=1.14; II,IV,V,VI=1.05	II, II/III
15	I,II=18.76; II=14.95; I,II,II/III=10.05; I,II,II/III,V=9.87	I, II
16	VII=10.88; VI=9.80; IV=4.90; II/III=4.43; VI,VII=2.92; IV,VII=2.77; IV,VI=2.52; III=2.49; II/III,VII=2.44; V=2.10; VIII=1.76; V,VI=1.64; IV,VI,VII=1.62	Indet.
17	VII,IX=16.66; VI,VII,VIII,IX=14.47; VI,VII,IX=13.50; VII,VIII,IX=11.52	VI, VII, VIII, IX
18	VI,VII,VIII,IX=22.24; VII=14.52; VI,VII,IX=13.38	VI, VII, IX
19	VI,VII,VIII,IX=49.34; VI,VIII,IX=11.56	VI, VII, VIII, IX

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20	II/III=12.15; I,II,II/III,V,VI=8.46; I,II,II/III,V=7.76; I,II,II/III=7.20; II,II/III=6.50; II=6.04; I,II/III=5.85	I,II,II/III
21	II/III=18.96; II,II/III=8.17; II=8.11 I,II,II/III=7.56; I,II/III=7.28	II/III
22	I,II=24.89; II=11.79; I,II,II/III=9.12; I,II,V=8.87	I, II
23	I,II=28.42; II=15.24; I,II,V=11.30	I, II
24	I,II=40.78; II=18.75	I, II
25	II=20.00; II,V=16.32; I,II=15.60	II
26	II/III=14.68; II=9.87; II,II/III=6.65; I,II,II/III=6.25; I,II/III=5.82; I,II,II/III,V=5.56; I,II,II/III,V,VI=5.54	II, II/III
27	I,II,II/III,V,VI=11.48; II/III=11.14; I,II,II/III,V=7.48; I,II,II/III=7.36; II,II/III=7.14; II=6.30	I,II,II/III
28	II/III=15.18; II=13.42; I,II,II/III, V,VI=7.87; V=6.35; VI=5.94; II,II/III=4.85	II,II/III
29	II=21.41; II/III=17.30; VI=12.44	Indet.
30	VI=29.94; II=21.10	VI
31	II=26.55; VI=25.74	II, VI
32	VI,VII,VIII,IX=45.81; VI,VIII,IX=9.49	VI, VII, VIII, IX
33	II=66.17	II
34	VI,VII,VIII=35.46; VI,VIII=12.28; VI,VII=11.28	VI, VII, VIII
35	II/III=18.12; II=16.76; V=10.41; II,II/III=4.16; II/III,V=3.32	II/III
36	II/III=17.02; II=15.99; V=10.20; IV=4.03; II,II/III=3.49	Indet.
37	II=10.25; II/III=8.92; V=6.89; I,II/III=4.48; I,II=4.28; II,II/III=4.19; II/III,V=4.04; II,V=3.90; I,II/III,V=2.69; I,II,II/III=2.28	II/III
38	I,II/III,V=13.09; I,II/III=9.55; I,II,II/III,V=8.71; II/III,V=7.36; I,II,II/III=6.88; I,II=6.25	I,II,II/III
39	II=8.34; II,V=3.24; II,IV,V=2.84; II,II/III=2.78; II,IV,V,VI=2.76; I,II=2.70; IV=2.65; II,II/III,IV,V=2.38; II/III=2.38; II,II/III,III,IV=2.34; V=2.28; II,II/III,IV=2.13; II,II/III,III=2.13; II,VI=2.05; II,II/III,III,IV,V=2.03; II,III=2.00; IV,V=1.89; II/III,IV=1.83; II/III,IV,V=1.80	II
40	II=32.69; IV=13.14; I,II=8.55	II
41	IV=29.46; III=14.25; II=8.92	IV
42	III=27.41; II=9.67; IV=7.03; VI=5.13; II,III,IV,V,VI,VII,VIII=3.41	III
43	II,IV,V,VI,VII,VIII=14.54; II,V,VI,VII,VIII=6.78; IV,V,VI,VII,VIII=6.71; II,IV,V,VII,VIII=4.48; II,V,VII,VIII=4.40; II,V,VI,VIII=4.34; IV,V,VI,VIII=3.83; II,V=3.73; II,V,VI=3.64	II, IV, V, VI, VII, VIII
44	II/III=14.09; II=11.47; V=7.43; IV=5.87; III=5.87; VI=4.29 II,II/III=3.10	Indet.
45	II/III=12.45; III=10.87; II=9.10; II/III,III=4.67; IV=4.00; II,II/III=3.59; II,III=3.11; III,IV=2.67	Indet.
46	III=4.72; III,IV=3.13; II/III,III=3.12; II/III,III,IV=2.63; II/III,III,IV,VII=2.44; II,II/III,III,IV,VII=2.35; I,II,II/III,III,IV,V,VI,VII=2.26; II,II/III,III,IV=2.19; I,II,II/III,III,IV,V,VI=2.14; II,II/III,III,IV,V,VI,VII=1.91; II,II/III,III,IV,V,VII=1.84; II,II/III,III,IV,V=1.75; II/III,III,IV,VI,VII=1.73; I,II,II/III,III,IV,V=1.73; II/III=1.68; II,II/III,III,IV,VI,VII=1.58; II/III,III,VII=1.55; III,IV,VII=1.50; I,II,II/III,III,IV,V,VI,VII,VIII=1.49; II/III,III,IV,VI=1.48; II,II/III,III,IV,V,VI=1.44; II,II/III,III=1.40; IV=1.38;	II/III, III, IV

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	I,II,II/III,III,IV=1.25; III,IV,VI=1.24	
47	III= 8.53; I,II,II/III,III,IV,V,VI,VII=3.47; II,II/III,III,IV,V,VI,VII=3.11; I,II,II/III,III,IV,V,VI=2.64; II,II/III,III,IV,VII=2.52; I,II,II/III,III,IV,V,VI,VII,VIII=2.36; II,II/III,III,IV,V,VII=2.26; I,II,II/III,III,IV,V=2.09; III,IV=2.09; II,II/III,III,IV,V,VI=1.97; II/III,III=1.92; II,II/III,III,IV=1.86; I,II,II/III,III,IV,V,VII=1.82; II,II/III,III,IV,V=1.80; II/III,III,IV=1.68; II,II/III,III,IV,V,VI,VII,VIII=1.67; II,II/III,III,IV,VI,VII=1.64; II/III,III,IV,VII=1.58; II/III,III,IV,VI,VII=1.52; I,II,II/III,III,IV,V,VI,VII,VIII,IX=1.31; I,II,II/III,III,IV,VII=1.24; II,II/III,III,IV,VI=1.22	II, II/III, III, IV
48	I,II,II/III,III,IV,V,VI,VII=4.65; I,II,II/III,III,IV,V,VI,VII,VIII=4.23; II,II/III,III,IV,V,VI,VII=3.67; I,II,II/III,III,IV,V,VI,VII,VIII,IX=3.22; II,II/III,III,IV,V,VI,VII,VIII=2.78; I,II,II/III,III,IV,V,VII=2.40; I,II,II/III,III,IV,V,VI=2.32; II,II/III,III,IV,VI,VII= 2.28; I,II,II/III,III,IV,V,VI,VII,IX=2.19; II,II/III,III,IV,V,VII=1.91; II,II/III,III,IV,VII=1.77; II/III,III,IV,VI,VII=1.70; II,II/III,III,IV,V,VI=1.64; I,II,II/III,III,IV,V,VII,VIII=1.60; I,II,II/III,III,IV,V=1.46; II,II/III,III,IV,V,VI,VII,VIII,IX=1.41; II,II/III,III,IV=1.29; I,II,II/III,IV,V,VI,VII=1.24 II,II/III,III,IV,VI,VII,VIII=1.23; II,II/III,III,IV,V=1.22 II,II/III,III,IV,VI=1.21; II/III,III,IV,VII=1.17; II,II/III,III,IV,V,VI,VII,IX=1.17; I,II,II/III,III,IV,V,VII=1.14; II/III,III,IV=1.12	II, II/III, III, IV, V, VI, VII
49	I,II,II/III,III,IV,V,VI,VII,VIII,IX=25.45; I,II,II/III,III,IV,V,VI,VII,VIII=12.96; I,II,II/III,III,IV,V,VI,VII,IX=6.88; I,II,II/III,III,IV,V,VI,VII=6.39	I,II,II/III,III,IV,V,VI,VII,VIII,IX
50	I,II,II/III,III,IV,V,VI,VII,VIII,IX=65.33	I,II,II/III,III,IV,V,VI,VII,VIII,IX
51	II,II/III,III,IV,V,VI,VII,VIII=5.56; II,II/III,III,IV,V,VI,VII=4.87; II/III,III,IV,VI,VII=4.58; II,II/III,III,IV,VI,VII=4.35; II,II/III,III,IV,VI,VII,VIII=3.96; II/III,III,IV,VI,VII,VIII=3.60; II/III,III,IV,V,VI,VII,VIII=3.43; II,II/III,III,IV,V,VII=2.98; II,II/III,III,IV,V,VII=2.94; III,IV,VI,VII,VIII=2.56; II/III,III,IV,V,VI,VII=2.47; II,II/III,III,IV,V,VII,VIII=2.39; III,IV,V,VI,VII,VIII=2.20; II,II/III,III,IV,V,VI=2.12; II,II/III,III,IV,VI=1.89; II/III,III,IV,V,VII=1.83	II,II/III,III,IV,V,VI,VII
52	II,II/III,III,IV,V,VI,VII,VIII=12.14; II,II/III,III,IV,V,VI,VII=7.36; II,II/III,III,IV,VI,VII,VIII=5.52; II/III,III,IV,V,VI,VII,VIII=5.17; II,II/III,III,IV,VI,VII=4.98; II/III,III,IV,VI,VII,VIII=4.03; II,II/III,III,IV,V,VII,VIII=3.69; II,II/III,IV,V,VI,VII,VIII=3.50; II/III,III,IV,VI,VII=3.08; II,III,IV,V,VI,VII,VIII=2.80	II,II/III,III,IV,V,VI,VII,VIII

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53	IV,VI,VII,VIII=20.48; VI,VII,VIII=15.52; IV,VI,VIII=13.03; VI,VIII=11.23	IV, VI, VII, VIII
54	III=29.72; II/III=26.52	III, II/III
55	V=6.23; VI=4.34; V,VI=3.28; II/III=2.17; II,V=2.16; IV,V,VI=2.10; II/III,V=2.09; IV,V=2.02; IV=1.96; IV,VI=1.92; II=1.86; II,V,VI=1.85; II,II/III,V=1.78; II/III,IV,V=1.69; II,VI=1.53; II,II/III,IV,V=1.41; II,II/III,V,VI=1.33; III,IV,VI=1.28; II/III,III,IV,VI=1.23; VI,VII=1.21; II,IV,V,VI=1.18; II,II/III,IV,V,VI=1.14; IV,V,VI,VII=1.10; IV,VI,VII=1.09; II/III,III,IV,VI,VII=1.04; V,VI,VIII=1.02	V, VI
56	II/III=29.82; II=16.88; I,II/III=10.68	II/III
57	II/III=15.91; III=7.75; II=7.14; II/III,III=5.38; II/III,IV=4.27; IV=4.10; II,III=3.08; II,II/III=2.65	II/III
58	II/III=20.09; III=10.36; II=9.15; II/III,III=5.70; II,II/III=4.86	II/III
59	II/III=10.62; I,II/III=6.03; II/III,III=4.70; III=4.65; II/III,IV=3.89; II,II/III=3.30; II=3.25; II,II/III,III=3.01; II,II/III,III,IV=2.55; II/III,III,IV=2.47; IV=2.06	II/III
60	II/III=12.71; II=7.66; I,II/III=7.50; II,II/III=4.65; I,II=3.84; I,II,II/III=2.16; II,II/III,III=2.00; II,II/III,III,IV=1.92; II/III,IV=1.89; II,II/III,IV=1.81; II/III,III=1.64; II,II/III,III,IV,VII=1.52; II/III,V=1.45	II, II/III
61	I,II/III=29.71; I,II=18.81; II/III=12.71	I, II/III
62	I,II/III=28.29; I,II,II/III=24.34	I, II/III
63	II/III=7.90; II=7.66; II,II/III=5.58; II/III,IV=2.66; II,II/III,III=2.46; II,II/III,IV=2.45; II,II/III,III,IV=2.39; II,V=1.98; II,III=1.98; II,II/III,V=1.96 II/III,V=1.88; II/III,III=1.85; II,II/III,III,IV,V=1.83; II,II/III,III,IV,VII=1.81; II,II/III,III,IV,VI,VII=1.80; V=1.76; II,II/III,IV,V=1.74; II,II/III,III,IV,V,VI,VII=1.68	II, II/III
64	II=8.48; II,II/III=3.82; I,II=3.52; II,II/III,III,IV,V,VI,VII=3.51; II,II/III,III,IV,V,VI,VII,VIII=3.18; II,II/III,III,IV,VI,VII=3.16; II,II/III,III,IV=2.56; II,II/III,III,IV,VII=2.51; II,II/III,V=2.38; II,II/III,III,IV,VI=2.35; II,II/III,IV=2.33; II,II/III,III,IV,V,VI=2.23; II,V=2.18; II,II/III,IV,V=2.15; II,II/III,III,IV,V=1.99; II,II/III,III,IV,V,VII=1.87; II,II/III,III,IV,VI,VII,VIII=1.79	II, II/III, III, IV
65	II,II/III,III,IV,V,VI,VII,VIII=9.25; II,II/III,III,IV,V,VI,VII=6.80; II,II/III,III,IV,V,VII=3.74; II,II/III,III,IV,V,VI=3.70; II,II/III,III,IV,VI,VII=3.40; II,II/III,III,IV,V,VII,VIII=3.33; II,II/III,III,IV,V=2.68; II,II/III,III,IV,VI,VII,VIII=2.59; II,II/III,IV,V,VI,VII=2.52; II,II/III,IV,V,VI=2.43; II,II/III,IV,V,VII=2.41; II,II/III,IV,V,VI,VII,VIII=2.19; II,II/III,III,IV,VI=2.09; II/III,III,IV,V,VI,VII,VIII=2.03; II,II/III,III,IV,VII=2.03	II, II/III, III, IV, V, VI, VII

4. *Phylogeny and biome occupancy*



5 Conclusiones





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5

En esta tesis se han analizado los patrones macroevolutivos de las aves no passeriformes y la influencia de los diversos cambios ambientales en sus procesos de radiación, dispersión y adaptación a lo largo de los últimos 90 millones de años, con especial énfasis en el Cenozoico. Esto ha sido posible gracias a la gran cantidad de información ecológica y biogeográfica existente en la literatura. Sin embargo, también es cierto que paradójicamente este gran conocimiento biológico de las aves actuales contrasta con el apenas emergente, pero también creciente, conocimiento filogenético y paleontológico de los diversos grupos. Considerando esto, en este proyecto se emprendió la labor de integrar toda la información disponible para reconstruir una aproximación histórica a gran escala sobre cómo han evolucionado las aves modernas, y así conocer los posibles agentes promotores de diversos procesos que configuran la dinámica macroevolutiva de un grupo tan diverso, que muchas veces quedan enmascarados en otro tipo de trabajos a menor escala espacial o temporal.

Teniendo en cuenta que esta tesis doctoral abarca la macroevolución de las aves no passeriformes desde diferentes perspectivas espacio-temporales y escalas taxonómicas, considero pertinente exponer los principales hallazgos y aportaciones de cada capítulo independientemente.

Capítulo 2. Especialización ecológica y cambios climáticos globales como reguladores de los patrones evolutivos en aves no passeriformes.

La hipótesis del uso de los recursos, propuesta por E.S.Vrba, sugiere una conexión directa entre los cambios físicos que ha sufrido la tierra y los patrones de diversidad. De esta manera, los procesos de extinción y especiación de los grupos naturales están relacionados y son potenciados en diferentes momentos por cambios climáticos y procesos tectónicos. Mientras que hasta este momento esta hipótesis solo había sido

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contrastada con datos de mamíferos, Nuestros resultados, sugieren también una relación próxima entre estos procesos y los patrones macroevolutivos de aves no paseriformes. De acuerdo con lo establecido en la hipótesis, se ha encontrado una alta frecuencia de especies restringidas a la ocupación de un solo bioma (especialistas). Estas especies estarían principalmente asociadas a los biomas situados en los extremos climáticos (pluvisilva, desierto, estepa y tundra), los cuales históricamente han presentado diversos procesos de expansión, contracción y fragmentación en sus áreas de distribución debido a cambios climáticos. Los patrones predominantes de especialización ecológica asociada a biomas particulares fueron conservados independientemente del comportamiento migratorio de las especies. Sin embargo, es de anotar que las especies migratorias presentaron una ocupación biómica relativamente más amplia con respecto a las sedentarias. Asimismo, los resultados sugieren que la evolución de estrategias migratorias habría facilitado la diversificación y especialización de algunos linajes en biomas hostiles y con estacionalidad de recursos como sucede con muchas especies de estepa y tundra. Por otra parte, cuando fueron consideradas las diferencias tróficas, los especialistas de bioma son más abundantes entre los taxones herbívoros con respecto a omnívoros y faunívoros respectivamente. Finalmente, algunas excepciones al marco explicativo de la hipótesis parecen estar asociados con la biogeografía de los ambientes de montaña y a la heterogeneidad de hábitat asociada a la dinámica ecotonal entre la pluvisilva y el bosque seco tropical. El análisis y amplia consistencia de esta hipótesis, evaluada por primera vez para las aves en esta tesis doctoral, se suma a los hallazgos de otros trabajos con mamíferos en el respaldo de una hipótesis evolutiva que hasta el momento muestra un alto nivel explicativo.

Capítulo 3. *“Out of South America”: añadiendo fósiles y tectónica para una nueva historia biogeográfica de las aves modernas (Neornithes).*

Se han realizado diversos análisis de reconstrucción paleobiogeográfica a partir de una propuesta filogenética que incluye todas las familias actuales de aves no paseriformes y sus parientes extintos mejor conocidos, así como una amplia base de datos biogeográficos y mapas consolidada para 30 intervalos temporales, abarcando cerca de 90 millones de años. Se establecieron diversos modelos que permitieron conocer la relación e influencia entre diversos procesos históricos que han acaecido desde finales del Cretácico con diferentes episodios de dispersión, diversificación y extinción evidenciados en distintos linajes de aves durante diversos periodos de su historia

evolutiva. Los resultados obtenidos apuntan hacia la consolidación de Gondwana y específicamente Sudamérica, como centro de origen y diversificación de las aves modernas. Asimismo, nuestros resultados sugieren un relevante papel de África y Europa en la dispersión y posterior colonización de los linajes hacía los continentes del Hemisferio Norte. Esta ruta permitiría que muchos linajes desarrollaran una distribución geográfica muy amplia en un momento temprano de su historia evolutiva.

El modelo más robusto estadísticamente sugiere un papel muy relevante de la dispersión en los procesos de colonización y diversificación de muchos grupos. Igualmente, nuestro modelo macroevolutivo establece diversos momentos de aumento en las tasas de colonización, muchos de ellos relacionados estrechamente con importantes procesos globales a nivel biótico y abiótico. Tres importantes oleadas de dispersión son detectadas a lo largo de la historia evolutiva de las aves, la primera tendría lugar durante el Cretácico Superior por parte de linajes de Neornithes asociados con ambientes acuáticos y semiacuáticos, así como algunos cursoriales. Esta primera oleada sufriría un importante descenso hacia finales del Cretácico, en relación con la profunda crisis ambiental que causó la extinción de un amplio componente de la biota terrestre. La segunda estaría relacionada con las condiciones de calentamiento global durante el Paleoceno y el Eoceno que llevarían a la expansión de los ambientes tropicales hacia altas latitudes, ofreciendo un amplio abanico de nuevos nichos para la diversificación; esta sería más destacada en linajes arborícolas. La tercera fase de dispersión sucedería desde el Oligoceno superior hasta el Mioceno inferior y estaría protagonizada especialmente por linajes de aves marinas y playeras, así como de aves cursoriales y arborícolas adaptadas a los ambientes abiertos. Este proceso habría estado relacionado con la aparición de nuevas corrientes marinas relacionadas con el desplazamiento de masas continentales y asociadas al enfriamiento global y el desarrollo del casquete antártico durante el Neógeno, y en los ambientes continentales al desarrollo y posterior expansión de los biomas abiertos gracias a la evolución de plantas C4. Pese a que durante el Mioceno se estabilizarían muchos de los procesos de colonización, después del Mioceno Medio, con la consolidación de los regímenes climáticos estacionales en latitudes septentrionales muchos linajes adaptados exclusivamente a condiciones climáticas tropicales desaparecerían de Eurasia y Norteamérica y retraerían sus áreas de distribución hacía latitudes más ecuatoriales. Lo anterior habría configurado la amplia distribución tropical de muchos linajes de aves observada actualmente.

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Capítulo 4. *Una perspectiva filogenética sobre la ocupación y adaptación de las aves a diferentes biomas: Galliformes y Falconiformes como casos de contraste.*

Como se evidenció anteriormente, la dinámica histórica de los biomas se constituye como fundamental para comprender los procesos macroecológicos y macroevolutivos. En este capítulo se abordó una evaluación más profunda de la ocupación de los diferentes biomas, esta vez teniendo en cuenta la historia evolutiva de las especies de dos grupos de aves desde una perspectiva filogenética: Galliformes y Falconiformes. Esto nos permitió conocer qué factores ambientales y adaptativos pueden condicionar la ocupación y colonización de ciertos biomas. Asimismo, este aspecto nos llevó a analizar el concepto de ocupación biómica bajo la hipótesis de la conservación de nicho. Lo cual sería fundamental para comprender las diferencias en la diversidad que observamos en los diversos biomas, así como su relación con diversos aspectos específicos de la historia natural de los dos linajes. Los resultados obtenidos para ambos grupos son ampliamente coherentes con la conservación filogenética del nicho. Se observó una alta tendencia hacia conservar el bioma de ocupación ancestral en la amplia mayoría de los biomas; si bien los biomas extremos (excepto el desierto), como la pluviiselva, la estepa y la tundra presentarían los valores más altos de conservación, constituyendo como un importante respaldo filogenético a las hipótesis evolutivas discutidas en el capítulo 2. Desde una perspectiva histórica, nuestro análisis permitió establecer cómo diversos procesos climáticos de enfriamiento global y geológicos durante el Mioceno serían fundamentales en la adaptación y evolución de los nichos climáticos en diversos linajes dentro de los dos grupos estudiados. Es de destacar que pese a una ancestría claramente ligada a los ambientes tropicales, la evolución y predominancia que alcanzarían durante el Mioceno los biomas estacionales cálidos abiertos y semiabiertos, representados por los bosques secos tropicales y las sabanas, mostraría ser determinante en los procesos de diversificación de ambos grupos, y probablemente algunas de las adaptaciones fisiológicas desarrolladas en relación a estos ambientes habrían sido claves en la posterior colonización de otros biomas tanto tropicales como templados.

Finalmente, a través de los análisis realizados en los diferentes capítulos de esta tesis, se ha logrado profundizar en diversas cuestiones macroevolutivas de las aves mediante la potente integración de información filogenética, biogeográfica y paleontológica en un estudio que logra arrojar mayor luz sobre la evolución de las aves y sus patrones históricos de diversificación.

5.1 Reflexión final y perspectivas de futuro

A lo largo del desarrollo de esta Tesis Doctoral se ha evidenciado la gran necesidad e importancia de la integración de las diversas fuentes de información en un enfoque hacia la generación y contraste de hipótesis evolutivas más amplias y con mayor poder explicativo. Esto es fundamental para comprender la dinámica de la biota en su conjunto así como determinados patrones que no se evidencian en estudios a pequeña escala. Este trabajo consolida un escenario macroevolutivo para la evolución de las aves de alto valor explicativo, y que integra toda la información biótica y abiótica tanto del presente como del pasado. En este sentido nuestra aproximación en el estudio de la macroevolución de las aves propone un horizonte explicativo que pone de manifiesto la destacada similitud de la dinámica macroevolutiva de las aves con la ampliamente estudiada en los mamíferos, pese a que estos últimos poseen un registro fósil más rico y las aves son consideradas muchas veces más “independientes” ecológicamente hablando, debido a la capacidad voladora de la mayoría de sus especies. Lo anterior es destacable porque marca un importante precedente del papel que desempeñan los procesos históricos globales en la evolución de las biotas.

Aunque éste trabajo se constituye como un importante precedente, es un trabajo que como todo en ciencia, deberá ser revalidado. Nuevos y diversos datos continuarán saliendo a la luz; descubrimiento de nuevos fósiles, obtención de propuestas filogenéticas más amplias y más robustas, nuevas especies. El hecho de que la ciencia avance se constituye en una renovación constante. Con ello, nuestras hipótesis y nuestros planteamientos podrán ser respaldados o rechazados (espero que lo primero). Sin embargo, eso es lo bonito que tiene la ciencia, es dinámica y activa. En el caso particular de la paleontología y la biología evolutiva, donde trabajamos armando el *puzzle* del pasado, siempre tendremos nuevas preguntas e interrogantes por el sencillo hecho de que *nadie estuvo allí*; nuestros planteamientos son meras aproximaciones para tratar de reconstruir una historia natural. Es por eso nuestro deber que estas aproximaciones sean cada vez más rigurosas y precisas a la luz de los nuevos hallazgos. En este sentido, y sin temor a equivocarme, el crecimiento exponencial del estudio y desarrollo de nuevas técnicas filogenéticas esta llamado a aportar una información muy valiosa sobre las relaciones entre las especies a la vez que será la base para nuevos análisis macroevolutivos. Sin embargo, es importante fomentar una constante y creciente relación entre las filogenias y los fósiles, muchas veces estudiados

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independientemente. Parafraseando a Einstein: “*las filogenias sin los fósiles están ciegas y los fósiles sin las filogenias están cojos*”.

Conocer los patrones históricos de cómo han respondido las avifaunas ante los diferentes cambios ambientales que sucedieron en el pasado es fundamental para evaluar hipótesis en biología de la conservación, dado el contexto del actual cambio climático. El gran conocimiento de las avifaunas como importantes componentes de la biodiversidad actual puede ser complementado por el procedente del estudio los procesos del pasado, de esta manera se pueden generar predicciones más precisas sobre la respuesta ecológica de especies y comunidades. Asimismo, este trabajo logra evidenciar que las aves pueden ser tan dependientes y susceptibles frente a los cambios ambientales como otros grupos animales. Siendo estos cambios y variaciones, los principales agentes configuradores de sus patrones de diversidad.

Desde el momento en que esta tesis fue planteada fui plenamente consciente del gran reto que suponía integrar una cantidad ingente de información para ver los patrones de la evolución a gran escala. Confieso que habría querido realizar muchas más cosas que se quedan en el tintero a la espera de nuevos hallazgos fósiles y de filogenias más completas. Personalmente espero que en un futuro no muy lejano pueda contribuir en ambos campos. Durante el desarrollo de esta tesis doctoral descubrí que en realidad el registro fósil de las aves puede aportar una información fundamental, la cual es *real* y directa, nos da idea de una ocupación biómica y geográfica ancestral. Es cierto que existe una importante diferencia en el conocimiento de las aves del pasado en diversas regiones del mundo, sin embargo ese no debe ser un impedimento para emplear la valiosa información que nos aportan. Nuestras inferencias pueden ser un importante punto de partida para la búsqueda de nuevos fósiles, los cuales ayudaran a su vez en hacer más sólidas y precisas nuestras aproximaciones.

Las aves, esos dinosaurios actuales tan apasionantes, aún guardan las repuestas a muchas preguntas que hoy siguen abiertas. Cómo evolucionan las diversas estrategias dietarias, reproductivas y comportamentales, o cuáles son los procesos que llevan a la amplia diversidad morfológica de sus picos, son sólo algunas de ellas. Sin embargo hay muchas incógnitas que sólo pueden ser respondidas a la luz de nuevos fósiles, y afortunadamente el registro de las aves está creciendo significativamente. La paleornitología es un campo emergente que aspira no sólo a la simple descripción clásica de los nuevos hallazgos. Cada vez son más abundantes los trabajos donde se aplican a los fósiles novedosas metodologías de análisis y nuevas inferencias paleoecológicas comienzan a emerger a partir del estudio de las avifaunas del pasado.

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En general, cada vez más la paleontología y la biología evolutiva generan explicaciones en un contexto integrador, comienzan a abrir nuevas líneas de investigación hacia el estudio de la evolución desde una perspectiva más integral y holística. Me alegraría formar parte de esta tendencia...



